

Universidad Arturo Prat
Iquique, Chile

und

Alfred-Wegener-Institut
für Polar- und Meeresforschung
Bremerhaven, BRD

**DISTRIBUTION PATTERNS, TROPHIC RELATIONSHIPS
AND STOCK INTERACTIONS IN THE
DEMERSAL FISH ASSEMBLAGE OFF CENTRAL CHILE**

vorgelegt von

HUGO ARANCIBIA

Dissertation
zur Erlangung des Doktorgrades
der Naturwissenschaften
(Dr. rer. nat.)
des Fachbereiches Biologie der Universität Bremen

Bremen 1989



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ABSTRACT

The demersal ichthyofauna on the continental shelf and upper slope off central Chile was studied in order to find out how it is spatially and temporally distributed. Two boundaries, at 100 m and 250 ± 50 m depth, limit three fish assemblages: inshore on the continental shelf, offshore on the continental shelf, and on the upper slope. *Merluccius gayi* and *Coelorinchus aconcagua* are the most important species both above and below the deepest boundary. Seasonal changes in connection with the movements of water masses and the anticyclonic center of high pressure over the southeastern Pacific Ocean are revealed.

The type of data obtained with bottom trawl surveys as well as the use of multivariate methods for their analysis are taken into account and are discussed, because these methods have rarely been applied in studies of the demersal fish fauna. The special problem of the statistical significance of a similarity index has also been considered.

Trophic relationships of ten species of fish were studied

using data obtained from two bottom trawl surveys carried out in March and November 1984. Intra- and interspecific overlaps change both temporally and spatially. Low values of trophic heterogeneity in almost all size classes analysed reveal the stenophagous character of the investigated fish. Significant exceptions from this rule are *Coelorinchus aconcagua* and the size group 36-50 cm total length in *Merluccius gayi*. Ontogenetic changes in feeding with growth were evident and were analysed in detail in *M. gayi* and *Hippoglossina macrops*. Specific prey size preferences were documented in several predator species following a log-normal frequency distribution of predator weight/prey weight. The most important associations of intra- and interspecific size classes have been shown by using the concept of "ontogenetic ecological units".

The consumption of *Pleuroncodes monodon* by *M. gayi* and *H. macrops* was estimated for two months in 1984 in the area between 35°45' S - 37°10' S. The method of Diana (1979) was applied to calculate the daily ration (DR) of both fish species, taking ontogenetic trophic units into account. In *M. gayi*, DR ranged from 0.0% to 0.10 % wet body weight (%BW) in March (beginning of autumn), and from

0.34 to 0.46 %BW in November (late spring). In *H. macrops*, DR ranged from 0.21 to 0.73 %BW in March, and from 0.29 to 0.59 %BW in November. The consumption of *P. monodon* by *M. gayi* was 42.2 t in March and 213.5 t in November. *H. macrops* consumed 627.6 t in March and 93.6 t in November. Assuming that the consumption values calculated in this work are representative of each of the two seasons (autumn-winter and spring-summer), the consumption of *P. monodon* by *M. gayi* and *H. macrops* is estimated at 18% of the standing stock of this crustacean in 1984.

KURZFASSUNG

Die räumliche und zeitliche Verteilung der demersalen Fischfauna des Kontinentalschelfs und des angrenzenden oberen Kontinentalhanges vor Zentral Chile wurde untersucht. Das Untersuchungsgebiet läßt sich in drei Bereiche mit jeweils typischer Zusammensetzung der Fischfauna unterteilen: (1) Küstennah auf dem Kontinentalschelf, (2) küstenfern auf dem Kontinentalschelf und (3) am oberen Kontinentalhang. Die Grenze zwischen diesen Gebieten verläuft in 100 m und 250 ± 50 m Wassertiefe. In den Gebieten (2) und (3) sind *Merluccius gayi* und *Coelorinchus aconcagua* die wichtigsten Fischarten. Saisonale Änderungen im Vorkommen der Arten wurden zurückgeführt auf Wasserströmungen und die Verschiebung des antizyklonischen Hochdruckgebietes über dem südöstlichen Pazifischen Ozean. Für die Untersuchung wurden Daten mittels der "Grundschleppnetz-Fischerei" gesammelt und diese mit Hilfe multivariater Methoden analysiert. Das spezielle Problem der statistischen Signifikanz eines "Ähnlichkeits-Index" wurde diskutiert.

Es wurden die trophischen Beziehungen von zehn Fischarten untersucht. Dazu wurde das Datenmaterial der Grundschlepp-

netz-Proben aus den Monaten März und November ausgewertet. Zwischen- und innerartliche Überschneidungen in der Nahrung ändern sich sowohl zeitlich als auch räumlich. Fast alle untersuchten Größenklassen zeigen eine sehr homogene Nahrungszusammensetzung und können als stenophag klassifiziert werden mit Ausnahme von *Coelorinchus aconcagua* und der Größengruppe 36-50 cm (Totallänge) von *Merluccius gayi*. Die ontogenetischen Veränderungen im Fressverhalten wurden von *M. gayi* und *Hippoglossina macrops* im Detail untersucht. Charakteristische Präferenzen der Beutetiergröße, die eine logarithmische Abhängigkeit zwischen Räuber- und Beutegewicht ergaben, wurden für mehrere Räuberarten beschrieben. Die wichtigsten Verbindungen von zwischen- und innerartlichen Größenklassen wurden mit Hilfe des Konzepts der "ontogenetisch-ökologischen Einheiten" aufgezeigt.

Der Wegfraß von *Pleuroncodes monodon* durch *M. gayi* und *H. macrops* wurde im März und November 1984 im Gebiet zwischen $35^{\circ}45' S$ - $37^{\circ}10' S$ bestimmt. Mit der Methode von Diana (1979) wurde die tägliche Ration (DR) beider Fischarten auf der Basis ontogenetischer trophischer Einheiten berechnet. Bei *M. gayi* lag die DR im März (Herbstbeginn)



zwischen 0,07 und 0,10% des Körperfeuchtgewichts (% BW), und im November (Spätfrühling) zwischen 0,34 und 0,46% BW. Bei *H. macrops* lag die DR im März zwischen 0,21 und 0,73% BW, und im November zwischen 0,29 und 0,59% BW. Der Wegfraß von *P. monodon* durch *M. gayi* betrug im März 42,2 t und im November 213,5 t. *H. macrops* konsumierte 627,6 t im März und 93,6 t im November. Vorausgesetzt, daß die berechneten Werte dieser Arbeit für jede der beiden Jahreszeiten (Herbst-Winter und Frühling-Sommer) repräsentativ sind, läßt sich der Wegfraß von *P. monodon* durch *M. gayi* und *H. macrops* auf 18% des "standing stock" dieser Crustaceen-Art für das Jahr 1984 veranschlagen.

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- A: Achira zone
 - B: Bio Bio zone
 - C: Exterior zone

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A: Achira zone
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1. INTRODUCTION

1.1. General Considerations.

The trawl fishery on the continental shelf and the upper slope off central Chile has a long history. From the 1930s, the most important species has been Chilean hake (*Merluccius gayi*; *Gadiformes: Merlucciidae*), caught along a coast line of nine degrees of latitude, from 30° S to 39° S. But in the same area red shrimp (*Pleuroncodes monodon*) and yellow shrimp (*Cervimunida johni*), both *Crustacea Anomura* of the Family *Galatheidæ*, and pink shrimp (*Heterocarpus reedi*; *Natantia: Pandalidae*) have also been fished.

The fisheries of Chilean hake and crustaceans have been strongly reduced during the recent years. Now Chilean hake landings range from 1/4 to 1/3 with regard to the 1960s, and those of crustaceans from 1/12 to 1/15 compared to 1979, the year with the maximum landing of *P. monodon* and *C. johni*.

At present the trawling fishery in central Chile based on *Pleuroncodes monodon* is carried out almost exclusively in

an area of $1^{\circ}30'$ of latitude ($35^{\circ}45' S - 37^{\circ}10' S$; Fig. 1). Both the Subsecretaria de Pesca (Undersecretariat of Fisheries) and the Instituto de Fomento Pesquero (Fisheries Development Institute) perform almost yearly monitoring surveys to evaluate the standing stock of *P. monodon* in the areas where it is still possible to find catchable densities of this crustacean. In the same areas *M. gayi*, black ling (*Genypterus maculatus*; Ophidiidae: Ophidiiformes) and bigeye flounder (*Hippoglossina macrops*; Bothidae: Pleuronectiformes) are caught as by-catch. All species of fish cited prey on *P. monodon*, as reported by BAHAMONDE and CARCAMO, 1959; HENRIQUEZ and BAHAMONDE, 1964; ARANA and WILLIAMS, 1970; BAHAMONDE and ZAVALA, 1981; MELENDEZ, 1983; ARANCIBIA *et al.*, 1986; ARANCIBIA, 1987; and ARANCIBIA and MELENDEZ, 1987.

Present views state that "... the rational and scientific management of fisheries must depend on a fundamental understanding of fish biology and ecology; that is what sort of animal fish are, and where and how they live ..." (PITCHER and HART, 1982). In this sense, the classical monospecific analyses in fisheries are replaced by multi-specific analyses. These analyses are especially carried



Fig. 1. Location of the trawling fishery off central Chile and principal landing ports (modified from BAHAMONDE *et al.*, 1986).

out within the framework of the International Council for the Exploration of the Sea, based on DAAN's work on consumption of North Sea cod (1973, 1975) and the theoretical work of ANDERSEN and URSIN (1977), among others. Basically, as pointed out by CADDY (1985), it is an important strategic consideration for fisheries research and management to define the trophic linkages.

Consequently, this work deals with:

- i.- The distribution of the ichthyofauna in the area of the fishery of *Pleuroncodes monodon*.
- ii.- The trophic relationships of the demersal ichthyofauna.
- iii.- The trophic interactions among the stock of *M. gayi*, the stock of *H. macrops*, and that of *P. monodon*.

1.2. General Objectives.

The general questions to be answered in this work are:

- 1.- How segregated is the demersal ichthyofauna temporally and spatially ?
- 2.- How does the ichthyofauna use the trophic resources ?
- 3.- How much is the predation of *P. monodon* by *M. gayi* and *H. macrops* ?

1.3. Thesis Outlined.

This work deals with the spatial and temporal relationships of the demersal ichthyofauna in the fishing area of *P. monodon*, the trophic relationships of this ichthyofauna, and the interactions among the stocks of Chilean hake (*M. gayi*), bigeye flounder (*H. macrops*), and *P. monodon*.

In Chapter 1, antecedents about the trawl fishery off central Chile are given, e.g. a short description of the study area including the topography and the sedimentology, the meteorology, and the characteristics of the water masses.

The subjects referred in the first paragraph are independently analysed in the Chapters 2, 3, and 4, each of them with its own introduction, materials and methods, results and discussion. In Chapter 5 the main results and conclusions of this study are summarized. The bibliography is given only once.

1.4. Short Description of the Bottom Trawl Fishery in Central Chile.

On the continental shelf and upper slope off central Chile (30° S - 38° S) (Fig. 1) an important trawl fishery is

concentrated, focussing mainly on *M. gayi*, *H. macrops*, *G. maculatus*, *P. monodon*, *C. johni* and *H. reedi*. Other species (with no commercial interest for the trawl fishery) are also caught as by-catch, including *Trachurus murphyi*, *Coelorinchus aconcagua*, some skates (*Raja chilensis*, *Bathyraja* sp.), little sharks (*Aculeola nigra*, *Centrosyllium nigrum*), and several crustaceans (*Cancer* spp., *Libinia* spp.).

Two kinds of fishing are performed in the demersal fishery: one concentrates on *M. gayi*, having as by-catch *G. maculatus* and *H. macrops*, and the other on crustaceans with an important by-catch of *M. gayi*. The principal landing ports are, or have been, Coquimbo (in Region 4 of the Chilean official nomenclature); Valparaíso, San Antonio and Quintero (in Region 5), and Talcahuano, San Vicente and Tomé (in Region 8).

1.4.1. The fishery on *Merluccius gayi*.

M. gayi has been recorded between 24° S and 47° S, but its fishery is localized between Coquimbo (30° S) and Corral (39° S). The commercial fishery began in 1939 (AGUAYO and ROBOTHAM, 1984). In the 1960s the landings reached

100,000 t per year (AGUAYO and YOUNG, 1982), whereas they amount only to at about 30,000 t at present. At the beginning of this fishery, until the 1970s, the principal landing ports were in Region 5. Their landings have, however, gradually decreased and therefore the fishing fleet operates now at greater distances from the ports (YANEZ, 1974). According to AGUAYO and ROBOTHAM (*op. cit.*), who performed analyses of the fishery of *M. gayi* between 1960 and 1982, this species has shown a progressive reduction of the stock, which is associated with a decrease of the recruitment sizes from 1966 to 1973; a tendency to stabilization is observed from the latter.

National landings and that of Region 8 of several fish resources are shown in Fig. 2 for the period 1970 - 1986. The landings of *T. murphyi* are due principally to the pelagic fishery in the region. The relative importance of Region 8 is significant in *M. gayi*, *G. maculatus* and *T. murphyi* (Fig. 3).

1.4.2. The Fishery on Galatheids (*P. monodon* and *C. johni*) and Other Crustaceans.

According to BAHAMONDE *et al.* (1986), the Chilean galatheid fishery began in 1953 and was entirely based on

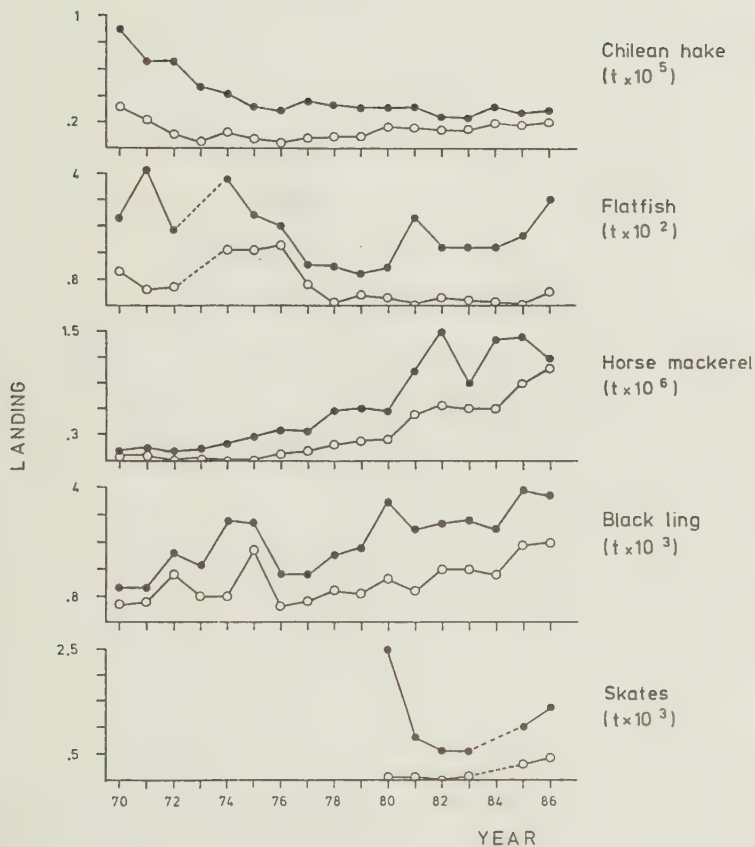


Fig. 2. Annual landings of demersal fish, 1970 - 1986 (Key: dots = national landing; circles = Region 8 landing. Source: National Fisheries Service (SERNAP, Chile).

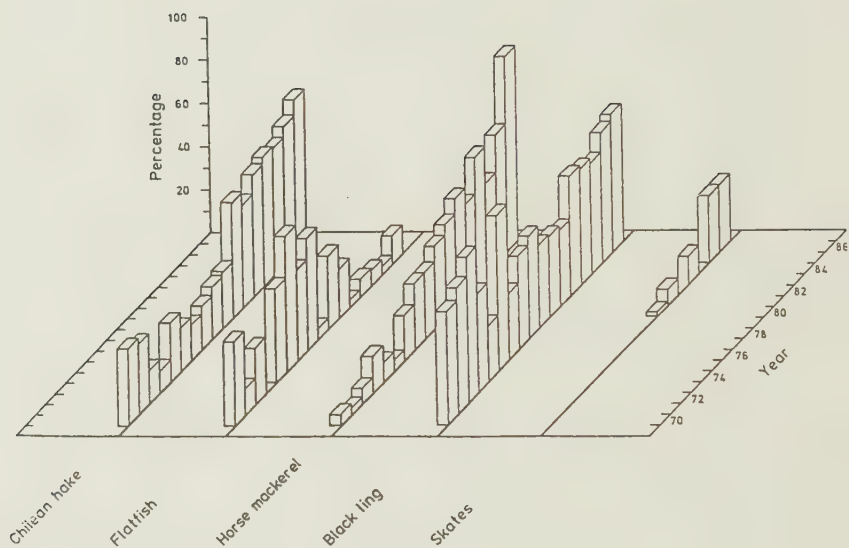


Fig. 3. Relative importance of the Region 8 landings in relation to the national landings for fish resources.

landings of *C. johni* made at Coquimbo, Valparaíso and San Antonio (Fig. 1). Landings peaked at 14,400 t in 1965 and fishing ranged from 29°30' S to 35° S in 1966. Subsequent landings of *C. johni* declined to 3,800 t in 1970. The abundance of this crustacean gradually decreased in the area between Coquimbo and Valparaíso but catches of *P. monodon* increased as the fishing fleet moved further south (Fig. 4). In 1967, landings of the latter species amounted to 4,600 t, increasing to 10,000 t in 1968, and to 23,300 t in 1969. From 1970 to 1975 the landings of *P. monodon* declined because of the redistribution of the fleet and not to a decrease in its abundance (BAHAMONDE *et al.*, *op. cit.*). Peak landings of 62,700 t in 1976 occurred when the industry began to market a processed product. This fishery was unregulated until 1979, when a prohibition of fishing for two months was imposed and then maintained until 1982. Since 1979, the fishery is concentrated in reduced zones (Fig. 5). Since 1983, the fishery has been regulated by quotas; the quota for 1986 was 4,830 t. The national landings of crustaceans and those of Region 8 are shown in Fig. 6 for the period 1970-1986. The fishery on galatheids collapsed in 1979, and at present the quotas are principally harvested in Region 8 (Fig. 7).

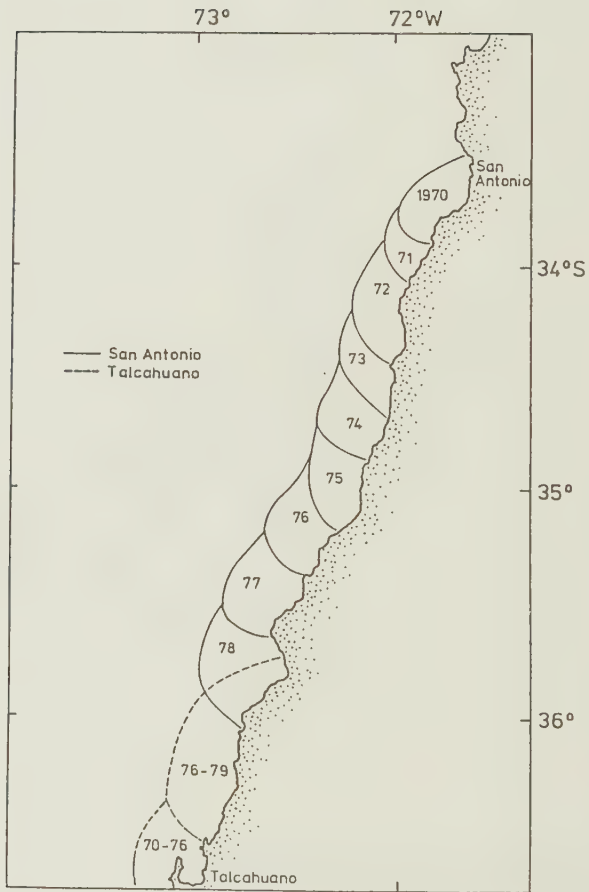


Fig. 4. Galatheid fishing fleet operating areas from 1970 to 1979 (PAVEZ and PENAILILLO, 1985).

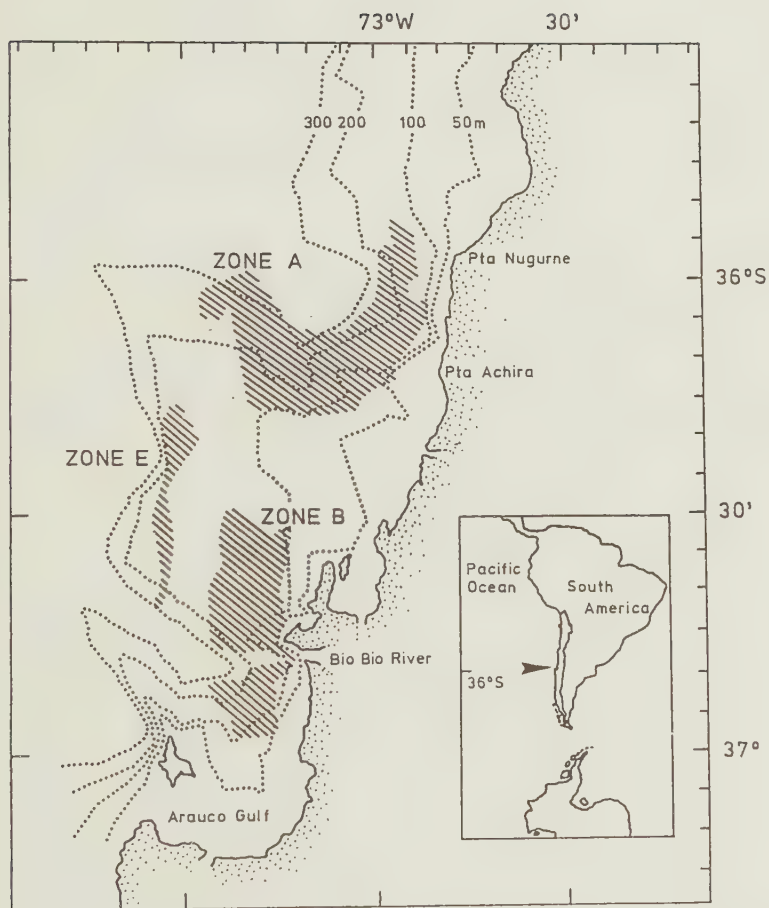


Fig. 5. Geographic stock distribution of *Pleuroncodes magadori* on the continental shelf and the upper slope off central Chile (ARANCIBIA, 1988).

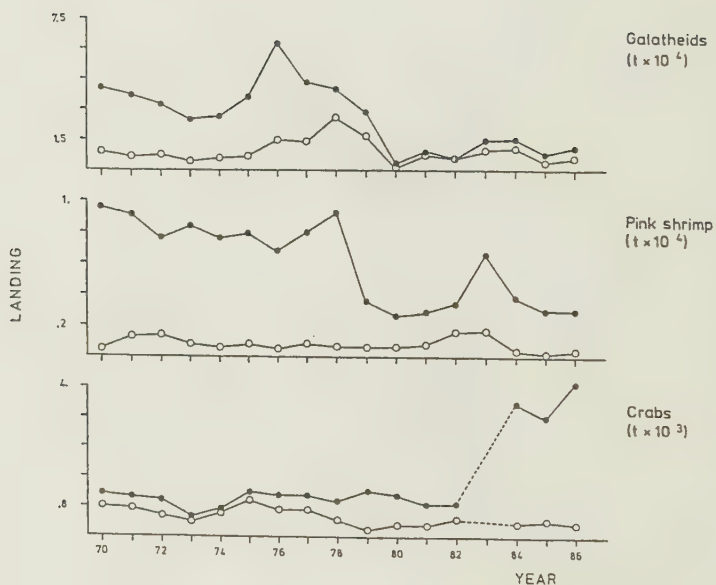


Fig. 6. Annual landings of crustaceans 1970-1986 (Key: dots = national landing; circles = Region 8 landing). Source: National Fisheries Service (SERNAP, Chile).

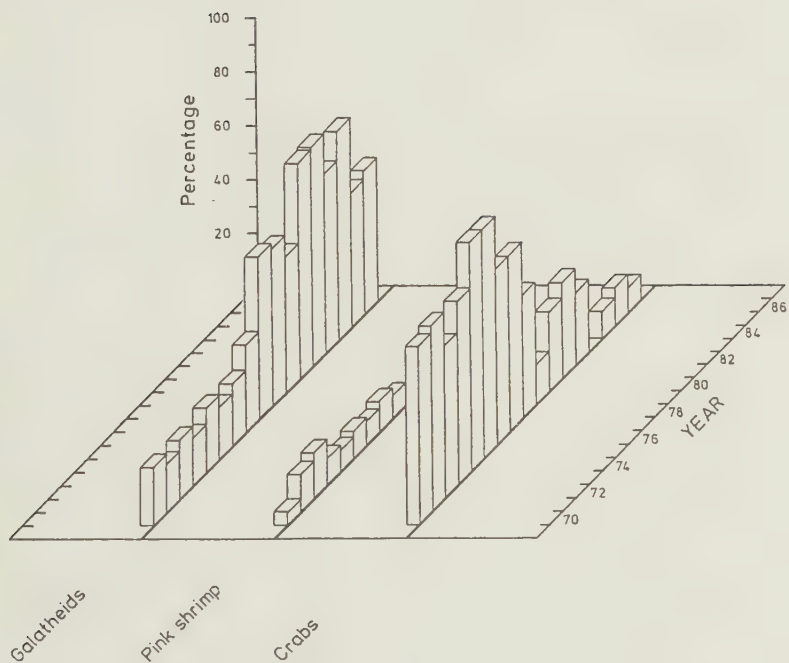


Fig. 7. Relative importance of the Region 8 landings in relation to the national landings for crustacean resources.

The fishery on *H. reedi* is not significant and is not regulated. The fishery on crabs is insignificant for the industry although it may be important for the artisanal fishery.

1.5. Description of the Study Area.

1.5.1. Topography and Sedimentology.

The study area is located between latitudes $35^{\circ}45'$ S and $37^{\circ}10'$ S, on the continental shelf and upper slope off central Chile. The morphology of the sea bottom shows two canyons (Fig. 8): the Itata Canyon and the Bio Bio Canyon. Two terraces, Itata and Tumbes, are near each canyon. The Talcahuano Basin is located between these two terraces.

South of Punta Nugurne, following the isobath of 200 m in the Talcahuano Basin, fine sediment (mud) is prevalent. North of Punta Achira, between the isobaths of 50 m and 150 m, the sediments are coarser. The Tumbes Terrace, and probably the Itata Terrace too, exhibit a gravel sediment type. Around the border of the Bio Bio Canyon prevail very fine sediments.

1.5.2. Meteorological Characteristics.

In general, three centers of atmospheric pressure regulate

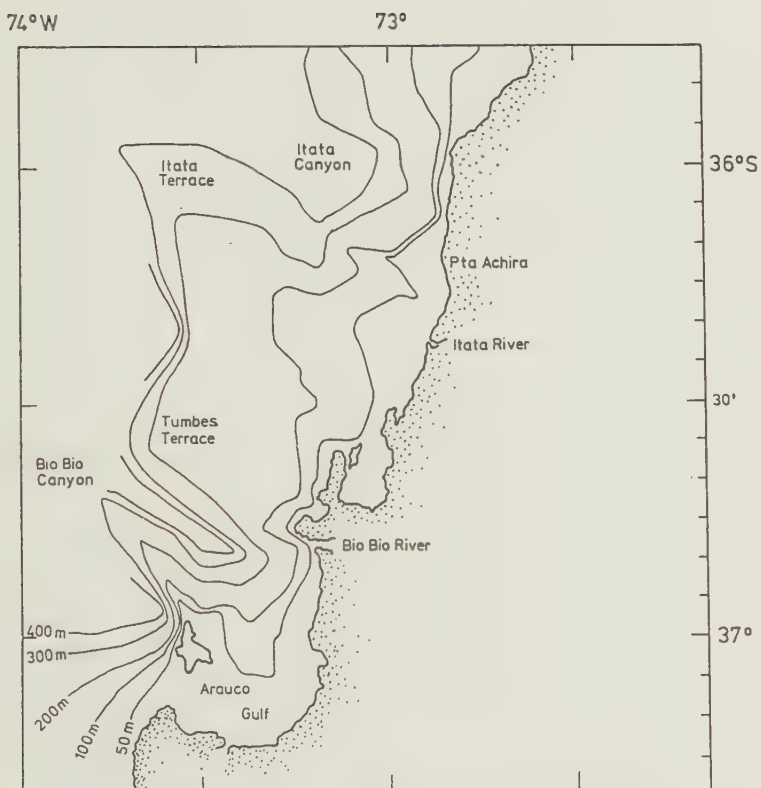


Fig. 8. Bathymetric chart of the study area (modified from GALLARDO *et al.*, 1980).

the meteorological conditions in Chile (Fig. 9): the anti-cyclonic high pressure center on the southeastern Pacific (A), the continental cyclonic low pressure center (D^0), and the austral cyclonic low pressure center (D^1). The center (A) is most important and regulates the others; it is normally localized between 90° W and 100° W, and moves further south, from 30° S to 40° S, in spring/summer. Its movement creates a thermal depression in central Chile (D^0), which is destroyed in autumn when the center (A) returns to its autumn/winter position (Fig. 10). The austral low pressure center (D^1) moves further south in summer and further north in winter.

1.5.3. Characteristics of the Water Masses.

In the study area, two main water masses are identifiable: Subantarctic Water (SAAW) and Equatorial Subsurface Water (ESSW) (BRANDHORST, 1971; SIEVERS and SILVA, 1975; Fig. 11).

Subantarctic water. This water mass is found at the surface and, due to its austral origin, it is characterized by moderate temperatures ($10^\circ - 18^\circ$ C), low but variable salinity ($32^\circ/\text{oo} - 34^\circ/\text{oo}$), oxygen values between 4.0 - 5.7 ml/l, and a maximum depth of 150 - 200 m offshore and 40 m near the coast, depending on latitude, season and the

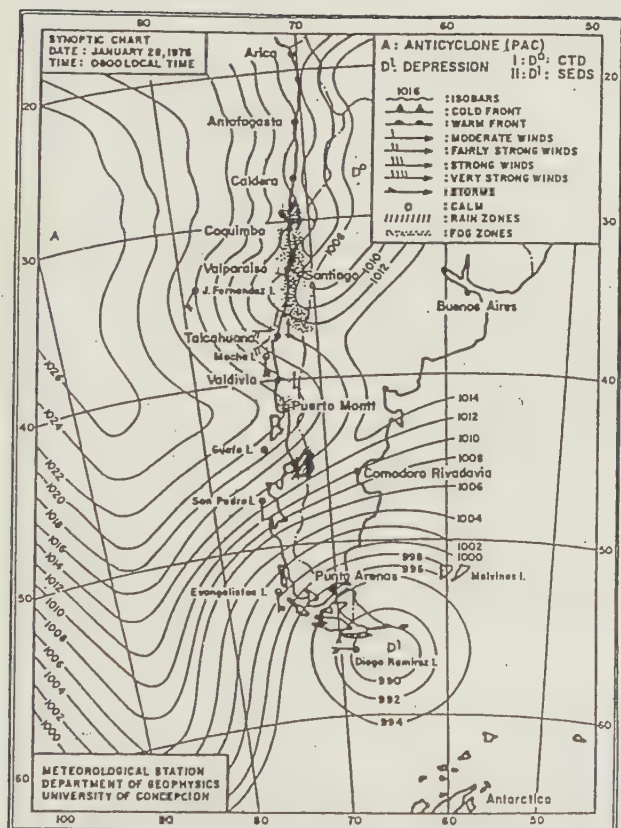


Fig. 9. Atmospheric pressure distribution on the south eastern Pacific Ocean during summer.

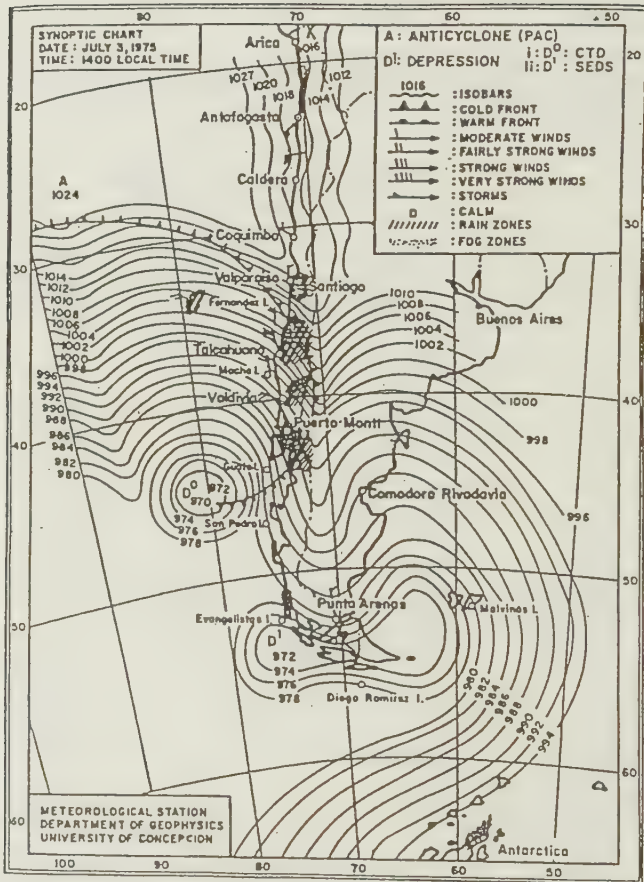


Fig. 10. Atmospheric pressure distribution on the south eastern Pacific Ocean during winter.

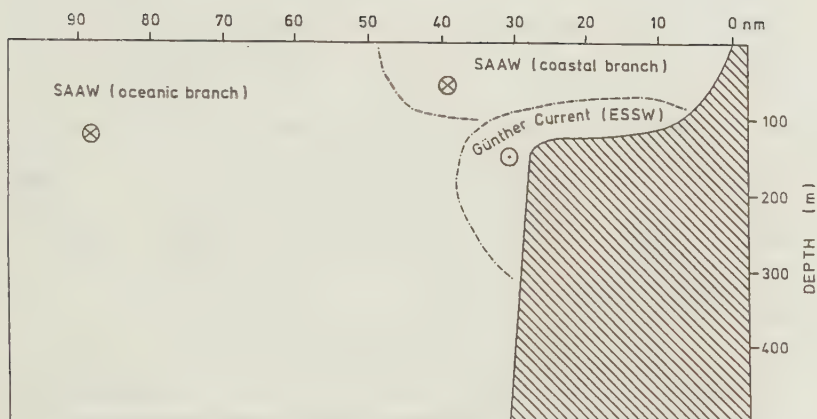


Fig. 11. Water masses distribution off central Chile (simplified picture).

contribution of continental waters. The SAAW has two branches: one between 75° W - 85° W, and another one between 73° W - 74° W.

Equatorial subsurface water. This water mass originates in the subsuperficial layers of the Equatorial Eastern Pacific and is characterized by temperature values between 7° - 13° C, relatively high salinity ($34.3^{\circ}/\text{oo}$ - $34.8^{\circ}/\text{oo}$), and very low oxygen values (0.1 - 2.0 ml/l). Its thickness varies between 200 and 350 m; its lower limit is located between 400 and 500 m depth. It moves southward, close to the coast.

1.5.4. Horizontal Coastal Circulation.

A relatively strong but narrow flow moving towards the equator corresponds to the Humboldt Current; it flows parallel to the coast and its extension westward ranges from 300 to 400 km. This water mass originates in Chile's austral region, and it corresponds to the SAAW. It is moving between the surface and 150 - 200 m depth, with velocities ranging from 12 - 18 cm/sec. This flow turns westward before 20° S (WOOSTER, 1970 *vide* SIEVERS and SILVA, 1975); according to WYRTKI (1963 *vide* SIEVERS and SILVA, *op. cit.*), this occurs between 13° S - 23° S.

In the coastal sector a poleward flow exists between 100 and 400 m depth. Its center has a velocity of 20 cm/sec. This flow corresponds to the Günther Current, also named Peru-Chile Counter Current, and it belongs to the ESSW. The austral limit is around 48° S (SILVA and NESHYBA, 1979).

1.5.5. Upwelling.

In north and central Chile upwellings occur when, in the season spring/summer (September-March), the trade winds are south and southwest (BRANDHORST, 1971; AHUMADA and CHUECAS, 1979; ARCOS and SALAMANCA, 1984; ARCOS and WILSON, 1984; Figs. 9, 10). Thus superficial waters are transported offshore, which causes a compensatory upwelling from subsuperficial waters. This water is rich in nutrients. During upwelling, the seasonal thermocline, located between 15 and 20 m depth, is broken, and subsuperficial waters (ESSW) can reach the surface (GÜNTHER, 1936). According to PETERSON *et al.* (1988), an active upwelling in central Chile is indicated by the presence of cool ($< 12.3^{\circ}\text{C}$), high salinity water ($> 34.6^{\circ}/\text{oo}$) with a low oxygen concentration (< 2.4 ml/l) at and near the sea surface. A typical active upwelling can last around 5

days, and periods of relaxed upwelling are indicated by warm water (SAAW) with higher oxygen concentration (temperature $> 14.2^{\circ}\text{C}$; salinity $< 34.3^{\circ}/\text{oo}$; oxygen $> 5.2 \text{ ml/l}$).

2. SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF THE ICHTHYOFAUNA.

2.1. Introduction

As mentioned in page 2, in the fishing area of *P. monodon* an important demersal ichthyofauna too is harvested as by-catch (HENRIQUEZ *et al.*, 1982, 1983; BAHAMONDE *et al.*, 1984). Work on demersal fish in this area have been done in a circumstantial context (e.g. OJEDA and CAMUS, 1977; 1977; BAHAMONDE and ZAVALA, 1981; MELENDEZ, 1983; BAHAMONDE *et al.*, 1984; ARANCIBIA *et al.*, 1986) but not aiming specifically at community analysis. Specific work about the distribution of commercial species are scarce and only that of YANEZ and BARBIERI (1983) can be considered in this context, who studied the distribution of the benthodemersal fauna in the area off Valparaíso ($32^{\circ}50' S$; $33^{\circ}10' W$). Periodical and seasonal investigations on this demersal fishfauna have, however, not been carried out.

In this chapter, the spatial (bathymetric) and temporal (seasonal) distribution of the demersal ichthyofauna in the fishing area of *P. monodon* will be analysed.

2.2. Materials and Methods.

2.2.1. On the origin of the information, samples, raw and standardized data.

The raw data were obtained from recorded captures of four bottom trawl surveys performed by the Instituto de Fomento Pesquero (IFOP; Fisheries Development Institute; Table I). The principal objective of these surveys was to estimate the standing stock of *Pleuroncodes monodon*. On board, the catch was separated by species and weighted. Time, velocity, depth and position of the trawl were also registered. All surveys were performed with R/V ITZUMI of the Subsecretaria de Pesca. As sampling gear, a shrimp trawl was used with 3 cm mesh in the cod-end, a 30 m headline equipped with floats, a 34.5 m footrope armed with rubber bobbins of 14 cm diameter and 14.8 cm width, doors of the "lucketa" type, and bridles 15 m long. Vertical opening varied between 2.8 and 3.4 m, while average horizontal opening between wind tips was measured as 11.75 m. In each cruise, around 150 bottom trawl hauls were carried out, in a depth range from ca. 30 to 350 m. All capture data were standardized per species, because both velocity and time of trawl were not constant (mean velocity: 4.1 km/h; mean actual time of trawling: 30 min).

The standardization of the capture has the form

$$C_{st} = C / d$$

where C_{st} = standardized capture, in kg/km;

C = actual capture, in kg;

d = trawling distance, in km, calculated from

$$d = v * t$$

where v = trawling velocity, in km/h;

t = actual trawling time, in h.

This type of standardization was also used by IFOP, as reported by HENRIQUEZ *et al.* (1982, 1983), BAHAMONDE *et al.* (1984) and ANONYMOUS (1984a), according to PALOHEIMO and DICKIE (1964) and ALVERSON and PEREYRA (1969).

2.2.2. Area of Study, Division by Zones and Bathymetry.

The area of study, where three discrete zones with catchable biomass of *P. monodon* can be recognized (Fig. 5), was arbitrarily divided into six depth strata per zone (Table II), according to ARANCIBIA (1988) and following the criterium of YAÑEZ and BARBIERI (1983), who used strata of 50 m depth. The number of samples per cruise and zone are given in Table III.

Each zone was independently analysed per cruise. Previous analysis without this separation did not show any clear patterns. In all analyses, species that occurred in more than 1% of the catches were considered. This reduced the number of 0-values that might have appeared as "noise" in the results (HAEDRICH and KREFFT, 1978).

2.2.3. Descriptive Parameters of the Community.

In order to describe the properties and distribution patterns of the demersal ichthyofauna, several classical community parameters were determined and the multivariate technique of cluster analysis was performed.

In community analysis, several numerical measurements must be considered because the patterns of a community can not be described by only one, and each describes a property of the community. It is very common to consider not only the number of species that a community contains but also the dominance structure, which is included in the applied diversity indices.

In this study, the following statistics and indices are used: number of species (S), Shannon-Wiener Diversity Index (H' ; SHANNON and WEAVER, 1949) and evenness (J' ;

PIELOU, 1975).

The definitions are:

$$H' = - \sum_{i=1}^S (p_i * \log_2 p_i)$$

where: p_i is the proportion of biomass in the i^{th} species.

$$J' = H' / H'_{\max}$$

The evenness is near 0 when the dominance is high and is 1.0 when all species are present in equal quantities.

$$H'_{\max} = \log_2 S$$

These statistics and indices were selected because the number of species and biomass are obvious measures to describe a community (PIELOU, 1969). The Shannon-Wiener index (H') combines the variety and evenness components as one overall index of diversity (ODUM, 1971). On the other hand, it seems to be the most consistent and useful method for obtaining significant diversity indices which are relatively independent of sample size (STIRN, 1981). As suggested by PIELOU (1969), it is desirable to distinguish between the two components of diversity: the species richness and the evenness. For this reason the evenness

index was also calculated. These statistics and indices were estimated with the computational program ACOM (NAVARRO, 1984).

2.2.4. Cluster Analysis.

Cluster analysis is a multivariate technique that permits the exploration of linkages between objects based on their attributes (variables), using a (dis-)similarity measure for the comparison. As a result, a classification often with a pictorial dendrogram of agglomerative hierarchical linkage between objects can be presented. The aim of this technique is to produce a number of tolerably discrete groups of patterns of cooccurrences (CLIFFORD and STEPHENSON, 1975). The objects are most homogenous within groups, while at the same time the groups are heterogenous among themselves as much as possible (ZUPAN, 1982). Each object can be represented as a point in a multidimensional measurement space. Mathematically it is a vector

$$\vec{x}_i = (x_{i1}, \dots, x_{in})$$

where the components are numerical values of the measurable properties. In this analysis, the units of sampling are bottom trawl hauls (Table III), the objects

are depths (Table II), and their attributes are the mean biomasses of each fish species per zone, expressed as percent. In this particular case, it is mathematically possible to express the object as the vector

$$\vec{x}_i = (\bar{x}_{i1} , \dots , \bar{x}_{in})$$

where $\vec{x}_i$ is the object (depth stratum from $i=1$ to m);

$\bar{x}_{ij}$ is the percent transformed mean biomass of each fish species (from $j=1$ to n) in each depth stratum.

In this case the matrix ($m \times n$) corresponds to m entities (depth strata) with n attributes. Each comparison was carried out between entities per cruise. A triangular similarity matrix ($m \times m$) was then generated in order to realize the classifications by means of cluster analysis. Czekanowski's Quantitative Index, CZ_{ik} , also named Bray Curtis Index (BLOOM, 1981) or Percent Similarity Index (VENRICK, 1983), was used as a similarity measure because it is perhaps the most widely employed quantitative measure in marine ecology, it is not affected by joint absences, and it has demonstrated to be useful in studies of marine ecology (BOESCH, 1977; FIELD *et al.*, 1982).

CZ_{ik} may be expressed as

$$CZ_{ik} = \frac{2 \sum_{i=1}^m \min (x_{ij} , x_{kj})}{\sum_{i=1}^m (x_{ij} + x_{kj})}$$

where x_{ij} is the occurrence of the j^{th} attribute in the i^{th} object; x_{kj} is the occurrence of the same attribute in the k^{th} object.

The unweighted pair-group method using arithmetic averages (UPGMA; also named group-average method) was used for classification because it is probably the most widely used clustering strategy (SNEATH and SOKAL, 1973) and introduces relatively little distortion to the relationships originally expressed in the inter - entity resemblance matrix (CUNNINGHAM and OGILVIE, 1972).

In order to establish a statistical criterium in the identification of groups between entities (depth strata), the similarity within entities was also recorded. Its mean was used as limiting value in the dendrogram. The comparison by pairs of samples (trawls) within depth stratum was arranged using a random numbers table; each

sample was compared only one time, i.e. the comparison was done without replace. The significance of difference within- and between depth strata of CZ_{ik} was tested by means of the Mann-Whitney U-test. This test can be applied because the type of measurement is ordinal and it can be arranged from smallest to largest. Previous analysis about the distribution of CZ_{ik} did not yield any known probability distribution. ARANCIBIA (1988) applied this test to the cluster analysis in order to establish a statistical criterium and, consequently, to avoid subjectivities in the choice of a similarity level (for details, see ARANCIBIA's paper (*op. cit.*) displayed to the 76th Annual Meeting of the International Council for the Exploration of the Sea; Statistic Committee, Ref. Demersal Fish Committee). The cluster analysis was performed with the program CLUST, supplied by Dr. D. Piepenburg from the University of Kiel.

2.3. Results.

2.3.1. Descriptive Parameters of the Community.

A superficial analysis of the more important species of fish caught in the fishing area of *P. monodon* shows a relatively scant number of species, with only a couple of dominants (Table IV). The mean number of species is very low in the Bio Bio zone although among years and zones there are differences. Similarly, in an overview, the diversity of biomass shows low values with, as expected, relatively high evenness (Tables Va, b, c).

Nevertheless, differences appear when the data are analysed with respect to depth strata. The number of species in all depth strata and zones is higher in November 1984 than in all other months (Fig. 12). In general, the Achira zone consistently shows the highest numbers of species, whereas the Bio Bio zone always exhibits the lowest values. In Achira, there is a tendency to find higher values of species number between 151-300 m depth; lower values at shallower depth occurred in Bio Bio.

The diversity of biomass (Fig. 13) is relatively constant in the Achira zone and the exterior zone; tendencies to

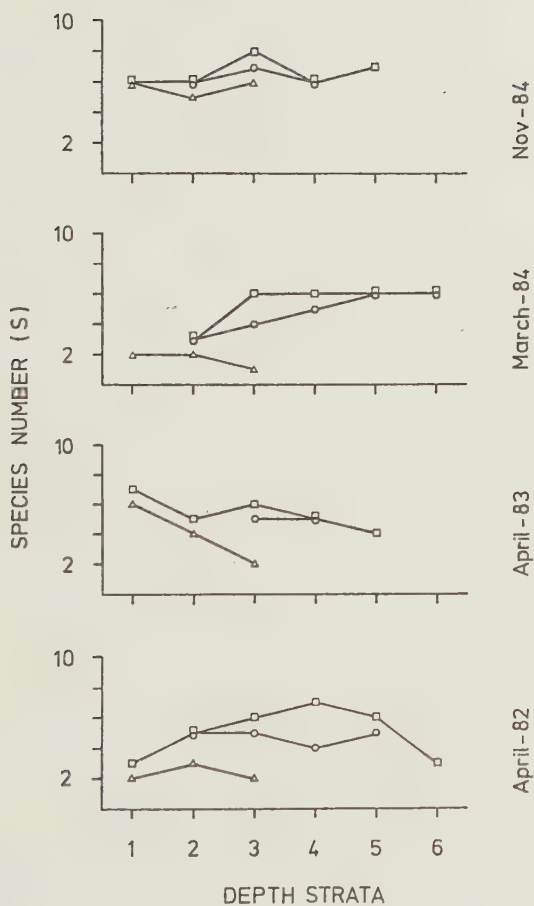


Fig. 12. Fish species number per depth stratum and survey (Key: squares= Achira zone; triangles = Bio Bio zone; circles = Exterior zone).

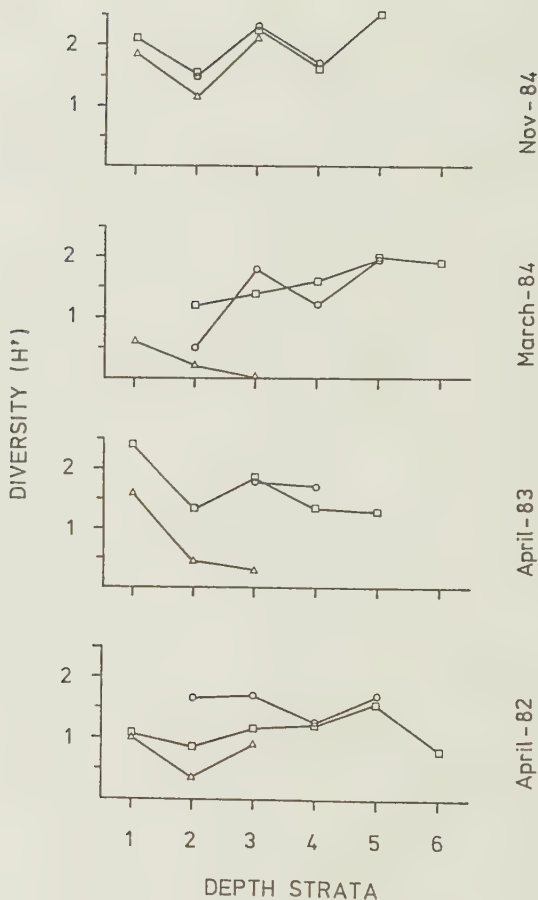


Fig. 13. Diversity of fish biomass per depth stratum and survey (Key: squares = Achira zone; triangles = Bio Bio zone; circles = Exterior zone).

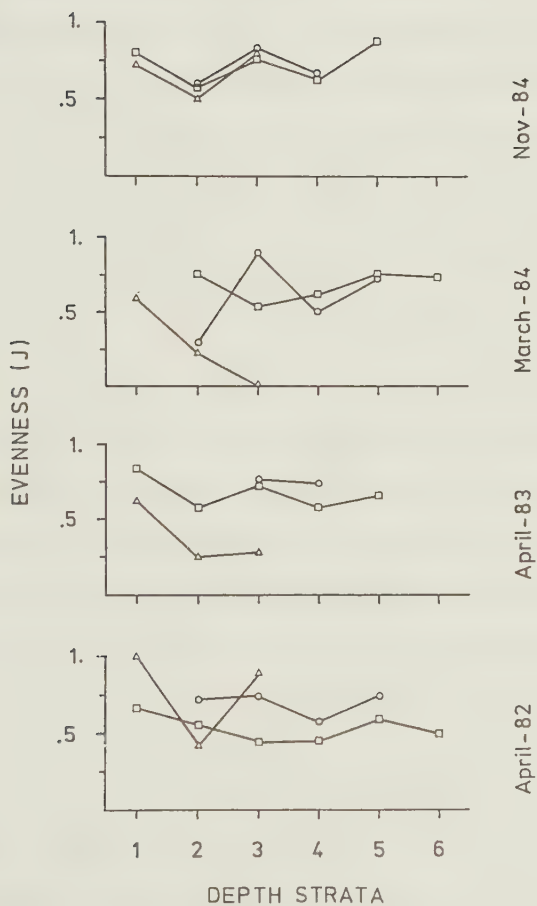


Fig. 14. Evenness of fish biomass per depth stratum and survey (Key: squares = Achira zone; triangles = Bio Bio zone; circles = Exterior zone).

increase with depth are revealed in March 1984 but to decrease with depth in April 1983. The Bio Bio zone shows the lowest values, and a tendency of diversity to decrease towards greater depths is revealed in April 1983 and March 1984. The evenness (Fig. 14) shows the same tendencies as H' .

2.3.2. Cluster Analysis.

2.3.2.1. April 1982.

Six groups can be recognized at a level of similarity within strata equal to 0.657 (Table VI a; Fig. 15 A). Moreover, each discrete group has its major species (Table VII a). Group 3 could be a heterogenous unit where a shift in the predominance of *M. gayi* by *C. aconcagua* can be recognized.

2.3.2.2. April 1983.

Three very distinct groups can be recognized at a level of similarity within strata equal to 0.615 (Tables VI b, VII b; Fig. 15 B). In group 1, *M. gayi* is the most important species. It is almost the exclusive species at strata B2 - B3, with secondary contribution of other species from strata A2 to A5. In group 2, the importance of *M. gayi* is secondarily shared with "Others". In group

3, both *M. gayi* and *C. aconcagua* contribute similarly as major species.

2.3.2.3. March 1984.

Six distinct groups can be recognized at a level of similarity within strata equal to 0.695 (Tables VI c, VII c; Fig. 15 C). In groups conformed by more than one stratum (groups 1 and 2), *M. gayi* is the main species. In the first, it is almost the exclusive species with presence of *G. maculatus*. This group was arranged with all Bio Bio zone plus E2. In the second group *M. gayi* dominates also, but with a gradually increasing contribution of *H. macrops*. The other groups are conformed by single strata - the deepest (E4, E5, A6) and the shallowest (A2) -, also with typical fish assemblages dominated by *C. aconcagua* and *T. murphyi*, respectively.

2.3.2.4. November 1984.

Four discrete, homogenous groups can be recognized at a level of similarity within strata equal to 0.581 (Tables VI d, VII d; Fig. 15 D). But either *M. gayi* (group 1) or *C. aconcagua* (group 4) are most important with partial exceptions in the shallowest strata (group 2). A gradual shift in the contribution of other species becomes

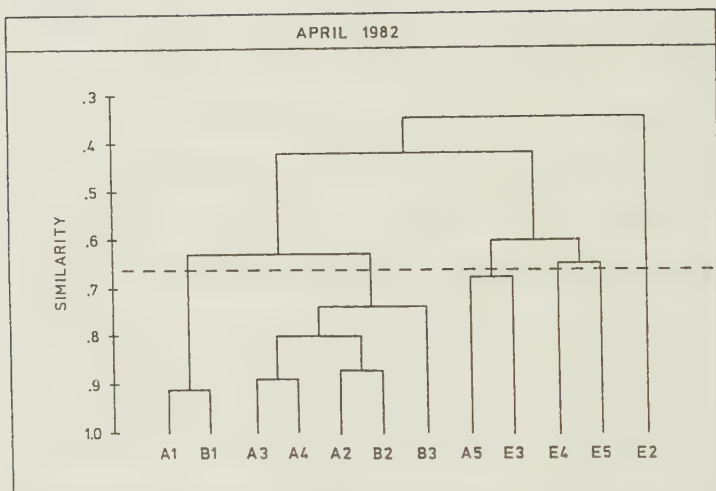


Fig. 15 A. Dendrogram showing classification of strata ($\alpha = 0.025$) based on catch data of demersal fish from bottom trawl survey carried out in April 1982. The broken line shows the mean level of similarity within strata (see Table VIIa for keys).

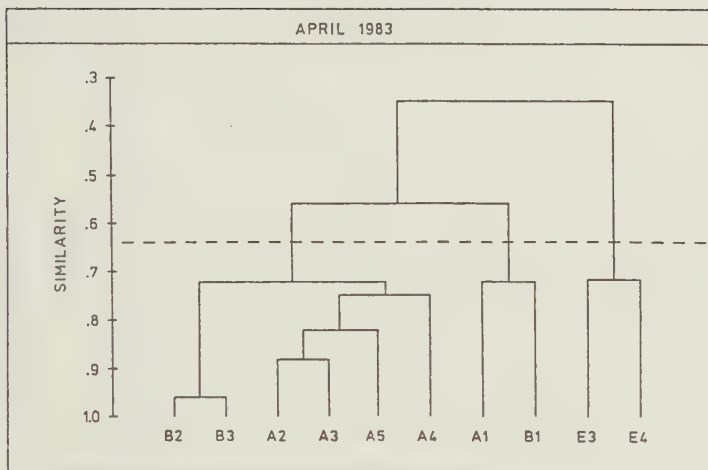


Fig. 15 B. Dendrogram showing classification of strata ($\alpha = 0.025$) based on catch data of demersal fish from bottom trawl survey carried out in April 1983. The broken line shows the mean level of similarity within strata (see Table VIIb for keys).

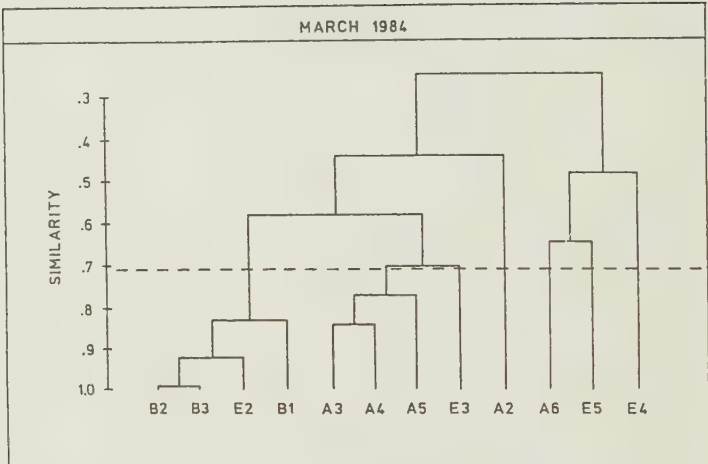


Fig. 15 C. Dendrogram showing classification of strata ($\alpha = 0.025$) based on catch data of demersal fish from bottom trawl survey carried out in March 1984. The broken line shows the mean level of similarity within strata (see Table VIIc for keys).

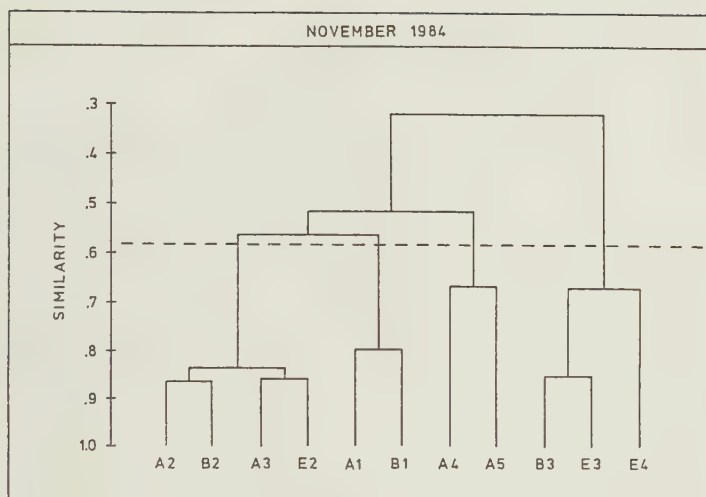


Fig. 15 D. Dendrogram showing classification of strata ($\alpha = 0.025$) based on catch data of demersal fish from bottom trawl survey carried out in November 1984. The broken line shows the mean level of similarity within strata (see Table VIId for keys).

apparent.

The strong connections of the demersal ichthyofauna among the strata per zones are evident, as can be seen in simple horizontal pictures (Fig. 16 A-D).

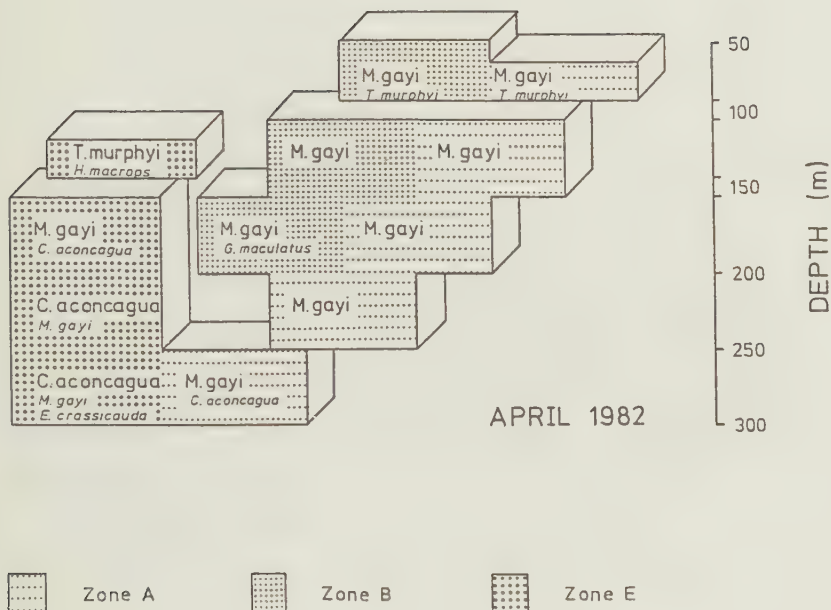


Fig. 16 A. Demersal fish assemblage on the continental shelf and the upper slope off central Chile in April 1982. The horizontal axis is an arbitrary distance westwards from the coast line.

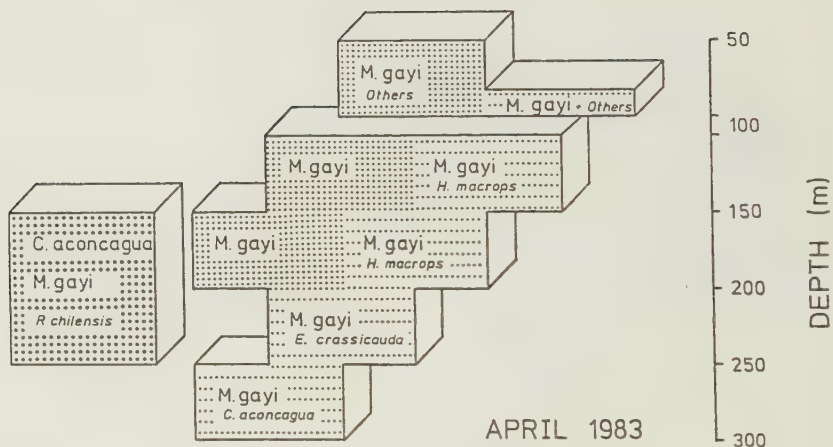


Fig. 16 B. Demersal fish assemblage on the continental shelf and the upper slope off central Chile in April 1983. The horizontal axis is an arbitrary distance westwards from the coast line.

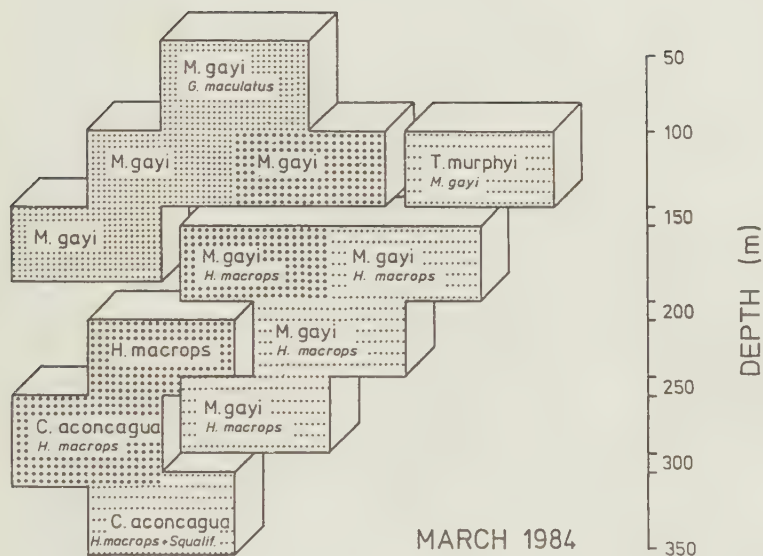


Fig. 16 C. Demersal fish assemblage on the continental shelf and the upper slope off central Chile in March 1984. The horizontal axis is an arbitrary distance westwards from the coast line.

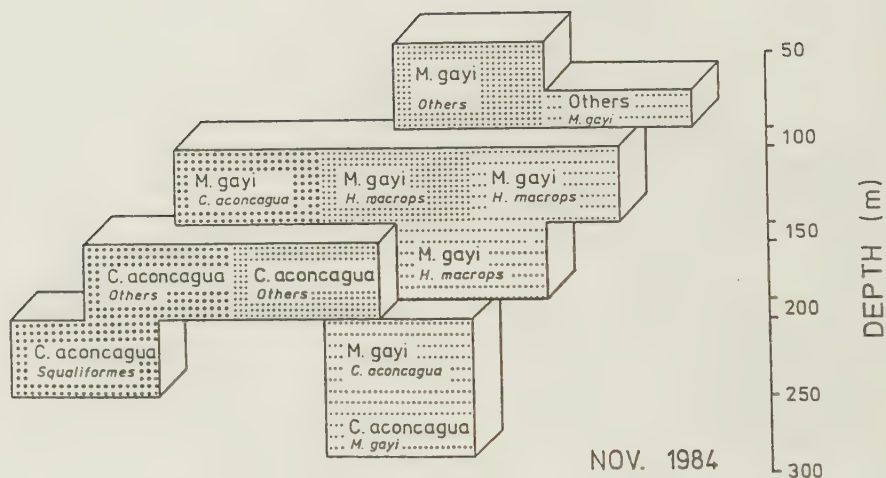


Fig. 16 D. Demersal fish assemblage on the continental shelf and the upper slope off central Chile in November 1984. The horizontal axis is an arbitrary distance westwards from the coast line.

2.4. Discussion and Conclusions.

The results allow to conclude that the demersal fishfauna on the continental shelf and upper slope off central Chile exhibits two important boundaries: one at depths of around 250 ± 50 m and one at depths of around 100 m. These two boundaries separate three distinguishable assemblages: one inshore on the continental shelf (above 100 m), one offshore on the continental shelf (between 100 and 250 ± 50 m, approx.), and one in the upper part of the continental slope.

Each assemblage is dominated only by a few species, therefore the total number of species is relatively low. *M. gayi* is most important offshore in association with *H. macrops*. Inshore, *M. gayi* is also the dominant species, but in association with pelagic and/or coastal fishes (e.g. *T. murphyi* and *P. jugularis*, respectively). On the upper slope *C. biconcava* progressively replaces *M. gayi*, in association with the bathypelagic fish *E. crassicauda*, skates or little sharks.

Despite the relatively distinct separation by depth, the ichthyofauna seems to be dynamic temporally as well as spatially. The results of the present study, as that of

OVERHOLTZ and TYLER (1985), show that the demersal ichthyofauna exhibits fluctuations during the year, and between years for the same season.

The causes of the type of zonation found off central Chile are not clear but both important ichthyofaunal boundaries can be correlated with physical changes in the substrate and in the water column (HAEDRICH *et al.*, 1975; 1980). In the study area, one boundary coincides with both the edge of the continental shelf and the presence of the Günther Current, formed by the Equatorial Subsurface Water (ESSW; SILVA and NESHYBA, 1979). At this boundary, the biggest concentrations of *M. gayi* are found. AVILES *et al.* (1979) proposed a strong relationship between the Günther Current and the presence of *M. gayi* in Chile; its seasonal migrations could be a consequence of the seasonal fluctuations of this current. The deficiency of oxygen in the ESSW is seemingly not a limiting factor for *M. gayi* (AVILES *et al.*, *op. cit.*), contrary to what was postulated by BRANDHORST (1959). Coincidentally, SAMAME *et al.* (1983) and ESPINO *et al.* (1985) communicated that in north Peru (5° S - 9° S), during "normal years", the biggest concentrations of biomass of *M. gayi peruanus* were found at

depths where the oxygen values ranged from 0.25 to 1.5 ml/l.

Above the boundary around 100 m depth, the presence of *M. gayi* is gradually reduced, and coastal or epipelagic species (*P. jugularis* and *T. murphyi*, respectively) increase. YAÑEZ (1974) reported a similar occurrence for the area off Valparaíso, in central Chile, being *P. jugularis* and *Stromateus maculatus* the most important species above 100 m depth. This shallower zone is affected by sub-antarctic water (SAAW) of the Humbolt Current.

Below the boundary at 250 ± 50 m depth, the presence of *C. aconcagua* increases. This change between hake (*Merluccius* sp. or an ecologically similar species) and rattail (*Coelorinchus* sp., or an ecologically similar species) correspond to zonations of demersal fish assemblages in comparable ecosystems. For instance, in the northeastern Atlantic, HAEDRICH *et al.* (1975, 1980) found a similar situation in the area off New England (*Urophycis regius* : *Coelorinchus carminatus*); DAY and PEARCY (1968), on the continental shelf and slope off Oregon (*Sebastodes* spp. : *Coriphaenoides pectoralis*); GABRIEL and TYLER (1980), in the area from Columbia River to Yaquina Bay, Oregon

(*Merluccius productus* : "ratfish"); SNELGROVE and HAEDRICH (1985), in the area off Newfoundland, northwestern Atlantic of Canada (*Gadus morhua* : *Coriphaenoides rupestris*); LLEONART and ROEL (1984), ROEL (1987), MACPHERSON and ROEL (1987), in the southeastern Atlantic off Namibia (*Merluccius capensis* : *Coelorinchus spp.*); and MACPHERSON (1981), along the coast off Catalonia, Spain (*Merluccius merluccius* : *Coelorinchus coelorinchus*).

In general, this study is in accordance with that of YAÑEZ and BARBIERI (1983), who found a marked discontinuity between the fauna of the continental shelf and that of the bathyal zone. Within each zone the faunal composition gradually changed with depth. Their study was carried out in the area off Valparaíso, Chile, where the family Macrouridae appears also at 220 m depth. It also reveals the presence of *M. gayi* between 150 - 300 m depth, but with conspicuous variation in the catch per unit of effort, both seasonally and bathymetrically, probably because of its migrations along central Chile. The coastal fauna was also found at depths shallower than 130 m, including *P. jugularis*, *C. callorinchus*, and the pelagic fish *T. murphyi*. Previously, YAÑEZ *et al.* (1974), YAÑEZ

(1974) and YANEZ and BARBIERI (1974) reported similar results for the sea bottom assemblage off Valparaíso.

There is another very interesting generalization in demersal fish assemblages of mid latitudes: only a couple of species contribute significantly to the fish catch. The case of the demersal fish assemblage of interest to this study is not an exception. Above 250 m, where trawling is carried out, only three or four commercially important species reach more than 80 per cent of the catch, independent of the season. Despite this, the other, mostly noncommercial, species perform essential roles in the ecosystem occupied by economically important fishes. As HORN (1980) pointed out, the noncommercial species may function as predators or competitors of exploited species, or otherwise affect community structure and, thus, indirectly influence economically important populations.

The characteristics of the exterior zone in this study must be emphasized. In an autumnal situation, i.e. April, the "axis" of this assemblage is located below 150 m, but with a characteristic fauna of the upper continental slope and isolated from the other two zones. After winter, i.e. November, associations are mainly found with the Bio Bio

zone. Before the rainy season, i.e. March, these connections change dramatically, and the association is mainly with the Achira zone. At this time, the system is displaced around 50 m upwards and towards the coast. This is likely to be correlated with, and synchronized to, the displacement of the anticyclonic center over the southeastern Pacific that is finally influencing the movements of the water masses in the region. ARCOS (1987) has shown that variation in the alongshore component of the winds induce a response in the hydrographic fields in central Chile.

I postulate in this work, following ARCOS (1987), that the spatial and temporal variability of the demersal fish biomass on the continental shelf and on the upper slope off central Chile is just a biological response to changes in hydrographic conditions related to the annual cycle of meteorological conditions. In spring/summer the trade winds are southwest, and in autumn/winter are north (see Figs. 9 and 10). As a result, superficial waters are transported offshore in spring/summer (mainly between October and March), which causes a compensatory upwelling from subsuperficial waters and, consequently, the dis-

placement upwards of still deeper waters.

2.5. Some Remarks About the Data and Methods.

Raw data from bottom trawl hauls are usually quite variable because of the heterogenous distribution of fish. A further source of variability for survey indices of abundance is the change in the catchability of a particular species with respect to the trawl survey from year to year, from season to season and even in the diel cycle (PENNINGTON and GROSSLEIN, 1978; PENNINGTON, 1986). Moreover, most of these fishes are considered to be demersal, although some are pelagic and swim just above the bottom as *T. murphyi*; others may migrate vertically, as *M. gayi* (VESTNES *et al.*, 1965 *fide* AVILES *et al.*, 1979), and occur near the bottom only during daytime (DAY and PEARCY, 1968). SNELGROVE and HAEDRICH (1985) concluded, through comparison with observations from submersibles, that trawling underestimates absolute abundance.

Then, the question is: What is considered to be the most representative data? What indices or measures can be used? At present, there is no agreement how this type of data must be handled.

In studies about demersal ichthyofauna, WIHLM (1968) has proposed to use biomass units in the Shannon-Wiener index (H'), as performed by LYONS (1981) and YAÑEZ-ARANCIBIA *et al.* (1985), because the number of individuals in the different species have been used with no consideration of weight among species. That means that individuals of different species of unequal weight would have an equal influence on a diversity index when the basic data were numbers of individuals, but would not have the same influence if data were in biomass units. H' is dimensionless and thus the choice of biomass units - as used in this study - will not influence the results. Moreover, in fisheries biology the variable biomass is more useful to compare and to analyse the importance of several species in the ecosystem. In this case, "biological activities" of the more important species can be well typified by using variables representing biomass.

It is considered in this work that H' is an useful index, because it permits the comparison of heterogeneity within and among zones. Moreover, it is possible to compare the heterogeneity with other areas and ecosystems for data obtained from bottom trawl hauls in demersal assemblages.

In this study, the mean of H' reveals that this demersal fish guild ($H' = 1.6$) is more heterogenous than a coastal Antarctic fish guild (H' less than 1.3; TARGETT, 1981) and, as expected, it is less heterogenous than those of tropical fish communities (H' between 2 and 3 or higher than 3; SMITH and TYLER, 1972 *vide* TARGETT *op. cit.*).

The literature about multivariate techniques in ecology is numerous, but just a little part has been applied to the analysis of demersal fish assemblages, due probably to the aggregated character of fish concentrations and the great mobility of fish. Usually the $\log(x+1)$ transformation is most useful for analyses of contagiously distributed species (CASSIE, 1967; STEPHENSON and DREDGE, 1976; YAÑEZ and BARBIERI, 1983). In this case, each bottom trawl haul can be used as a sample unit, which means that no information is lost, and analysis within areas, zones, strata, etc. can be performed.

Finally, something has to be said about the similarity index used here. Czekanowski's Quantitative Index has been largely used in community analysis because it has the great property of synthesizing information. ARANCIBIA (1988) discussed this index and suggested simultaneous

analyses between and within entities, taking the mean of the CZ's within entities as a limiting value. It appears that the determining process of calculating a limiting value equal to the mean of CZ within entities is no so bad and, at least, it is useful when we wish to analyse a dendrogram and test the significance of difference with the Mann-Whitney U-test. This procedure - as used in this study - appears to be adequate, but it needs further improvement.

3. TROPHIC RELATIONSHIPS IN THE DEMERSAL FISH ASSEMBLAGE OFF CENTRAL CHILE.

3.1. Introduction.

Only few studies about food and feeding of species of the demersal fish assemblage exist in Chile. Trophic relationships of fish off central Chile are largely unknown even though many species, such as *M. gayi*, *H. macrops* and *G. maculatus*, are of commercial importance. Moreover, non-commercial species have received almost no attention, such as *C. aconcagua*, *P. jugularis*, skates (*R. chilensis*, *Bathyraja* sp.), and little sharks (*C. nigrum*, *A. nigra*). Their biology too is almost unknown.

Most publications on feeding of fish off central Chile are relatively old and mainly descriptive (BAHAMONDE, 1950, 1953, 1954; BAHAMONDE and CARCAMO, 1959; HENRIQUEZ and BAHAMONDE, 1964; ARANA and WILLIAMS, 1970; ROSARIO, 1970; OJEDA and CAMUS, 1977; YANI *et al.*, 1977). During the 1980s only the following articles were published: BAHAMONDE and ZAVALA (1981), who studied the feeding of *Genypterus maculatus* and *G. blacodes*, that of MELENDEZ (1983), who studied the feeding of *M. gayi*, and that of

ARANCIBIA and MELENDEZ (1987), who described the feeding of ten species of fish. GALLARDO *et al.* (1980) described the feeding of seven species of fish but their work was not published. A lack of ecological approaches in most of the published works is the rule.

Almost all these papers focussed either on a single or only on a couple of species, with no consideration of interactions among species, although this type of research is widely regarded as too limited (MAY *et al.*, 1979). As TARGETT (1981) pointed out, this type of investigation gives information on the general feeding biology of individual species but does not give information on food resource partitioning or interactions among fish within communities obtaining prey from the same resource base. Furthermore, these studies have also given little information on dietary changes accompanying growth, with the exception of ARANCIBIA's paper (1987), who analysed in detail changes in feeding with growth in *M. gayi*.

Detailed studies of food resource utilization in fish assemblages are difficult to perform due to the fact that fish are highly mobile organisms in aquatic habitats (GROSSMAN, 1986) and that a significant degree of prey

variability may be due to size related changes, which indicate that inter- and intraspecific partitioning of energy resources vary with fish size (ROSS, 1978). On the other hand, feeding relationships among fish are considered to be an important factor regulating or at least affecting such features as abundance, growth, migration, etc. (DAAN, 1973, 1975; PAYNE *et al.*, 1987). This type of interactions can thus exert considerable influence on the population dynamics of stocks within a community (LAEVASTU and FAVORITE, 1980; CADDY, 1985). For this reason, quantitative feeding relationships of fish have received increased attention in recent years (HAHM and LANGTON, 1984; LIVINGSTON and BAILEY, 1985; MACPHERSON and ROEL, 1987; ROEL and MACPHERSON, 1988), especially in order to fit the parameter "predation mortality" in exploited species and, consequently, to improve the prediction capacity in assessment of fish stocks through multispecies analysis (ANONYMOUS, 1984 b; PENNINGTON, 1984; SHEPHERD, 1984; GISLASON and HELGASON, 1985; LLEONART *et al.*, 1985 a, b; MEHL, 1987; SPARHOLT, 1987; TJELMELAND, 1987).

The aim of this chapter is to analyse the trophic rela-

tionships of ten species of the ichthyofauna in the area of the fisheries on *P. monodon*, in March and November 1984, taking into account especially the feeding similarity between size groups of fish species and prey selection. Analyses on ontogenetic trophic units (*sensu* LIVINGSTON, 1982) in *M. gayi* and *H. macrops*, and also an attempt to establish ontogenetic ecological units (*sensu* MACPHERSON and ROEL, 1987) incorporating all fish species, was performed.

3.2. Materials and Methods.

3.2.1. Sampling and Laboratory Analysis.

4,762 stomachs of ten species (2,624 with stomach content) caught during two cruises in the area of the fisheries on *P. monodon* in March and November 1984 were studied. All samples were randomly obtained on board during diurnal time using bottom trawls.

On board, fish showing signs of regurgitation were discarded from the samples. Fresh swallowed organisms in the stomach were discounted as they had probably been taken while the fish was in the net (SMALE, 1984; BULMAN and BLABER, 1986). This problem is relatively easy to identify for major crustaceans because they move still in the stomach of fish at the moment of the sampling; for fish as prey, commonly their bodies remain incompletely ingested in the stomach. Fish were measured to the nearest centimeter (total length, TL, in all cases) and their sex identified. Stomachs were dissected, sealed and fixed in 10% buffered commercial formalin.

In the laboratory, stomachs were analysed individually. Prey items were sorted, identified to the lowest possible

taxon, weighted and counted. The excess of water was eliminated using blotting-paper. For major crustaceans, the cephalothorax length (CL, in mm) was recorded and for fish, the TL, in cm. According to the digestion state, prey were categorized into three types: 1 = complete, 2 = semi-digested, 3 = digested. Fish lengths were converted to weights and age by using published and own unpublished weight/length and length/age relationships. Species of fish were sorted by size classes according to previous analyses for *M. gayi* (ARANCIBIA, 1987) but taking also into account the published information about the length at first spawning of *H. macrops* and *M. gayi* (VOIGTH and BALBONTIN, 1981; BALBONTIN and FISCHER, 1981). The other species were eventually sorted by size classes, previous inspection of the feeding data matrix. If apparent differences were not recorded, the available sample of predator species was not sorted into size classes.

For each zone of study a sufficiently large number of stomachs per size class of all main predator species were analysed. ARANCIBIA (1987), using the "number of prey taxa/number of stomachs-curve" (MODDE and ROSS, 1983), demonstrated that a sample size of 7 - 28 specimens per

group in *M. gayi* is adequate to describe the diet of this species, as was also demonstrated by other authors for several species of fish (ROSS, 1978; LIVINGSTON, 1982; GROSSMAN, 1986). The length classes by species, the nomenclature used in the following analyses and the sample size are given in Tables VIII a - j and summarized in Table IX.

3.2.2. Description of the Diet.

In order to describe the diets of fish, the gravimetric method was used and then the wet weight per taxon was transformed into percentage. As HYSLOP (1980) pointed out, a single method of stomach analysis does not give a complete picture of dietary importance, but wet weight is probably the more convenient measure where large amounts of material are collected, and it is relatively easy to perform.

In this study, following BERG (1979), the "main food" category is the component of the fish diet that comprises the greatest proportion. In order to give a general indication of the relative extent of feeding heterogeneity of fish, the Shannon-Wiener index (H') was used. High values of H' are indicative of euryphagous fish species, and low

values are indicative of stenophagous species. No attempt to test statistically both categories through a limit value has been done, because the purpose is merely descriptive. In order to avoid data matrices with too many zeros (HAEDRICH and KREFFT, 1978), only prey taxa contributing equal to or more than 1% in wet weight by fish size classes were included in all following analyses.

3.2.3. Feeding Similarity.

Czekanowski's Similarity Index (CZ_{ik} ; see pages 29-31 for explanations about its application in this work) was used for quantifying the resource use between intra- and interspecific size classes of co-occurring demersal fish. For clustering of size classes the UPGMA algorithm (SNEATH and SOKAL, 1973) was applied. In order to eliminate intuitive criteria for judging the reliability of the inter-size classes overlap, as pointed out by WALLACE and RAMSEY (1983), the significance of difference of CZ_{ik} within vs. between size classes was estimated with the Mann-Whitney U-test (see pages 31-32 for explanations). PATTERSON (1986) noted that most, if not all empirical studies of dietary differences based on prey taxa, have not involved formal tests of statistic significance, probably because the form

of the data makes standard methods difficult to apply. For example, the distributions are usually far from normality, and show too much individual variation to allow a standard contingency table approach. Other statistical methods, as that suggested by SMITH (1985), have not been applied here because he erroneously assumed that prey types consumed by a single predator species have a Poisson distribution ($\mu = \sigma$); it was not here performed because the variance of the stomach contents of fish is greater than the mean.

3.2.4. Prey Size Selection.

Predator-prey size selection was investigated using the methodology of URSIN (1973), performed also by HAHM and LANGTON (1984) and URSIN and ARNTZ (1985 a, b, c). The size relationship between predator and prey is reflected in a score, derived from the natural logarithms of their weights, as

$$\text{SCORE} = \ln (w_i / w_j)$$

where w_i = predator weight and w_j = weight of an individual prey. According to CLARK (1985 b), weight of an individual prey was substituted for weight of one prey

taxon in w_j , as with small prey it was felt unrealistic to regard each individual prey in a stomach as a result of a single predator-prey encounter.

The frequency distribution of the predator's selectivity scores was graphed, and if approximately "normal", the distribution was described by its mean and standard deviation. Data were combined into 1.0 score intervals to clarify the overall shape of frequency distribution curves; each interval was represented by its mean point in the figures.

3.2.5. Ontogenetic Trophic Units (OTUs).

LIVINGSTON (1982) coined the term "ontogenetic trophic unit" to designate the size classes of a particular species that take the same preys. An attempt to define OTUs in *M. gayi* and *H. macrops* was made, because a large amount of data was available. For the first species, groups as communicated by ARANCIBIA (1987) were included into the analyses. In the second species three groups were arranged from previous inspection of the raw data of preys by length of predator, taking also into account the length at first spawning.

In order to analyse the distribution of OTUs per species (*M. gayi* and *H. macrops*, respectively), the multivariate discriminant analysis (DA) was performed. The raw feeding data were transformed to $\log(x + 1)$, where x = weight of prey taxon by individual fish, to remove the dependence of the variance on the mean (ELLIOTT, 1971), as performed by MACDONALD and GREEN (1986). DA was performed with the SPSS version X-2.1 (for some explanations, see Appendix 2).

3.2.6. Ontogenetic Ecological Units (OEUs).

MACPHERSON and ROEL (1987), following LIVINGSTON (1982), coined the term "ontogenetic ecological unit" to designate the intra- and interspecific size classes that feed on similar taxa, taking also into account the distribution and abundance of the predators. These authors, following SCHOENER's (1968) similarity index, developed the weighted overlap index (IND) which is applied in this work, attempting to disclose OEUs. IND is symmetric and ranges between 0 and 1. For any pair of species the index would be 1 if both fish species ate the same prey in equal proportion (by mass) and had the same spatial distribution and abundance. This index is defined as

$$IND_{ij} = 1 - \frac{\sum_k \sum_z (n_{ki} p_{kiz} - n_{kj} p_{kjz})}{\sum_k (n_{ki} + n_{kj})}$$

where p_{kiz} is the percentage (by mass) of prey z found in the stomachs of fish species i at depth stratum k ; p_{kjz} is the same percentage for fish species j at the same depth stratum; n_{ki} and n_{kj} are the abundance (by mass) of fish species i and j , respectively, at depth stratum k where at least one of the fish species is present. Cases of double absence are not computed by the index. In this analysis 10 fish species as predator (17 groups, in total), 6 depth strata, 46 prey taxa and two surveys, March and November 1984, were taken into account (for depth strata see Table II; fish species as shown in Tables VIII a-j and summarized in Table IX).

MACPHERSON and ROEL (1987) considered significant values of IND higher than 0.5. I regard this limit as too high because the similarity index used in this work to analyse only feeding similarities (CZ_{ik}) - being equivalent to that of SCHOENER (1968) and producing almost the same results - reaches with my data no values higher than 0.5. With the introduction in IND of the biomass as second

variable, obviously this index will reach lower values than 0.5. For this reason, an arbitrary value of 0.25 is considered to be reasonably significant. No attempt to test IND statistically has been made. As the catch was not completely sampled by length but completely weighted per species, it was supposed that the random samples of fish are representative, in proportion, to the abundance of fish in the sea. This information by size classes, plus that of mean biomass per species and depth strata used in chapter 2, permitted the approximate estimation of biomass by size classes, in kg.

3.3. Results.

3.3.1. Diet Composition and General Feeding Patterns of Individual Species.

3.3.1.1. *Trachurus murphyi* (horse mackerel; Table VIII a)

The main food of *T. murphyi* are Euphausiacea. Low values of H' , from 0 to 0.7, with a mean value of 0.3 (Table X), reveal the stenophagous character of this species.

3.3.1.2. *Epigonus crassicauda* (cardinalfish; Table VIII b)

E. crassicauda feeds mainly on Euphausiacea but it can also prey on larger, benthic crustaceans (*H. reedi*, *Pasiphaea* sp.) and juveniles of *M. gayi*. Nevertheless, low diversity values, from 0 to 1.6, with $\bar{H}'$ equal to 0.5 (Table X), reveal the stenophagous character of this species.

3.3.1.3. *Merluccius gayi* (Chilean hake; Table VIII c)

Seasonal and geographical changes are characteristic for the feeding patterns of *M. gayi*. Furthermore, ARANCIBIA (1987) pointed out that prey size (by weight) does increase exponentially with predator length. *Pleuroncodes monodon* is heavily predated at different predator size classes. Euphausiacea are the main food in the size group

26-35 cm, and their relative importance decreases with increasing fish length. The relative importance of pelagic fish (*Engraulis ringens* and *Scomberesox saurus*) increases in larger fish. Younger fish (17-25 cm) cannibalize postlarvae. A tendency for euryphagy can be recognized only in the size group 36-50 cm, whereas stenophagy is characteristic for all other size groups (Table X). The relative importance of each prey item varies in different areas, probably according to its local abundance in the fauna, exemplifying the hake's opportunistic feeding habits.

3.3.1.4. *Genypterus maculatus* (black ling; Table VIII d)

The main food of *G. maculatus* are benthic crustaceans (*P. monodon*, *Cancer* spp., *P. armata*) in all zones and seasons but fish are also consumed. Relatively low values of H' , from 0.7 to 2.3 and $\overline{H'}$ equal to 1.5 and 2.0 (Table X), reveal the stenophagous character of this species.

3.3.1.5. *Hippoglossina macrops* (bigeye flounder; Table VIII e)

P. monodon is largely the main food of *H. macrops*. Some changes are shown seasonally but basically the diet consists of this crustacean, with some contributions of

other large crustaceans (*C. johni*, *H. reedi*, *C. porteri*, *P. aramata*) but fish are also predated. Low values of H' , from 0.2 to 2.1, reveal the stenophagous character of this species. $\bar{H}'$ does decrease with length of fish (Table X).

3.3.1.6. *Coelorinchus aconcagua* (rattail; Table VIII f)

Changes in the main prey taxa of *C. aconcagua* between March and November are revealed. Polychaetes are the main food of *C. aconcagua* in March; in November it consists of small crustaceans, including postlarvae and juveniles of *P. monodon*. *C. aconcagua* has the highest H' values, ranging from 2.0 to 3.3 and $\bar{H}'$ equal to 2.7 (Table X); the feeding character of this species tends towards euryphagy.

3.3.1.7. *Raja chilensis* (Chilean skate; Table VIII g)

In the Achira and Bio Bio zones the main food taxa of *R. chilensis* are exclusively large crustaceans, but their relative importance varies according to the season. *P. monodon* is an important prey. *R. chilensis* can partially feed on fish. Low H' values show its stenophagous character, although H' does increase by a factor of two between March and November. $\bar{H}'$ is equal to 1.5 (Table X).

3.3.1.8. *Bathyraja* sp. (little skate; Table VIII h)

Large crustaceans are the main food taxa of *Bathyraja* sp., with a strictly carcinophagous, stenophagous character, with H' ranging from 1.4 to 1.7, and $\bar{H}'$ equal to 1.6 (Table X). The relative importance of each prey item changes geographically and seasonally. *P. monodon* is an important prey.

3.3.1.9. *Aculeola nigra* (hooktooth dogfish; Table VIII i)

Fish and large crustaceans are the main food of *A. nigra* in the Achira zone. In the Exterior zone large crustaceans are the main food. Low H' values, from 1.1 to 2.3, and $\bar{H}'$ equal to 1.7, reveal *Aculeola*'s stenophagous character.

3.3.1.10. *Centroscyllium nigrum* (combtooth dogfish; Table VIII j)

Only this species feeds significantly on lanternfish, but large crustaceans are also important. H' is equal to 2.0.

3.3.2. Trophic Associations.

3.3.2.1. Achira Zone.

Significant differences in food of fish in the demersal assemblage between and within groups were found (Tables XI a, b). Five major groups in March and three in November

1984 were recognized (Figs. 17 A, 18 A; Tables XII a, b). *T. murphyi*, *E. crassicauda* and *M. gayi* (26-35 cm) were sorted as pelagic predators. *C. biconcava* does remain trophically isolated in all arrangements. All size classes of *H. macrops* (11-40 cm) and one of *G. maculatus* (32-50 cm) are sorted as predators on large crustaceans. Morphologically similar species, as skates (*R. chilensis* vs. *Bathyraja* sp.) or sharks (*A. nigra* vs. *C. nigrum*), are clearly clustered in different associations but basically they are crustacean predators.

3.3.2.2. Bio Bio Zone.

Significant differences in food of fish within and between size classes were found only in March 1984 (Tables XI a, b). *M. gayi* (16-50 cm) -group 1- and *G. maculatus* (32-80 cm) -group 2- segregated clearly the food resources in terms of interspecific sorts. The largest individuals of *M. gayi* are trophically isolated (Fig. 17 B; Table XIII a). In November only *T. murphyi* is revealed as single pelagic predator. All other fish sizes do not show significant interspecific differences and mainly feed on *P. monodon* (Fig. 18 B; Table XIII b).

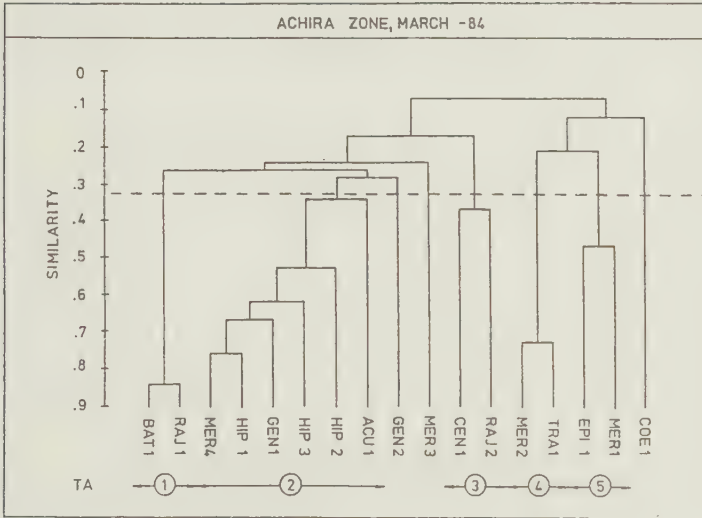


Fig. 17 A. Dendrogram showing classification of predators by size classes in the Achira zone (March 1984; $\alpha = 0.025$) based on wet weight (in percentage) of prey items. The broken line shows the mean level of similarity within size classes of predators. TA = trophic associations. See Table IX for identification of groups.

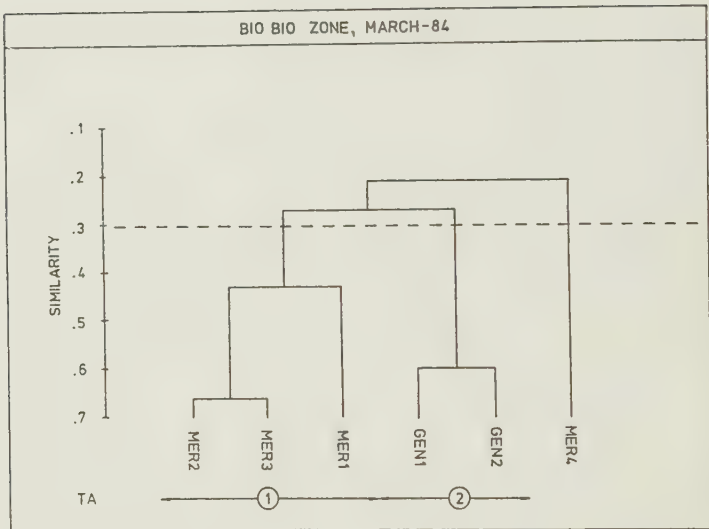


Fig. 17 B. Dendrogram showing classification of predators by size classes in the Bio Bio zone (March 1984; $\infty = 0.025$) based on wet weight (in percentage) of prey items. The broken line shows the mean level of similarity within size classes of predators. TA = trophic associations. See Table IX for identification of groups.

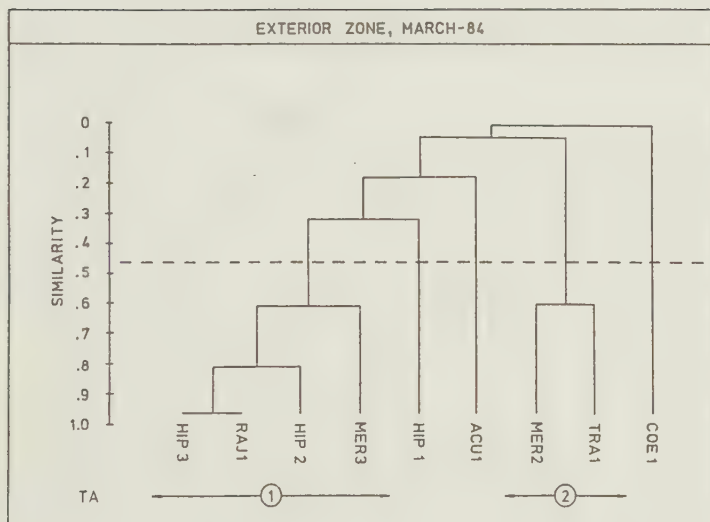


Fig. 17 C. Dendrogram showing classification of predators by size classes in the Exterior zone (March 1984; $\alpha = 0.025$) based on wet weight (in percentage) of prey items. The broken line shows the mean level of similarity within size classes of predators. TA = trophic associations. See Table IX for identification of groups.

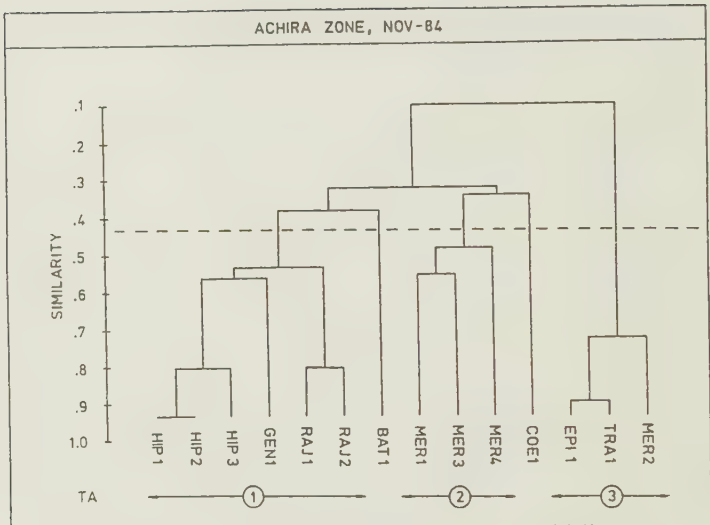


Fig. 18 A. Dendrogram showing classification of predators by size classes in the Achira zone (November 1984; $\alpha = 0.025$) based on wet weight (in percentage) of prey items. The broken line shows the mean level of similarity within size classes of predators. TA = trophic associations. See Table IX for identification of groups.

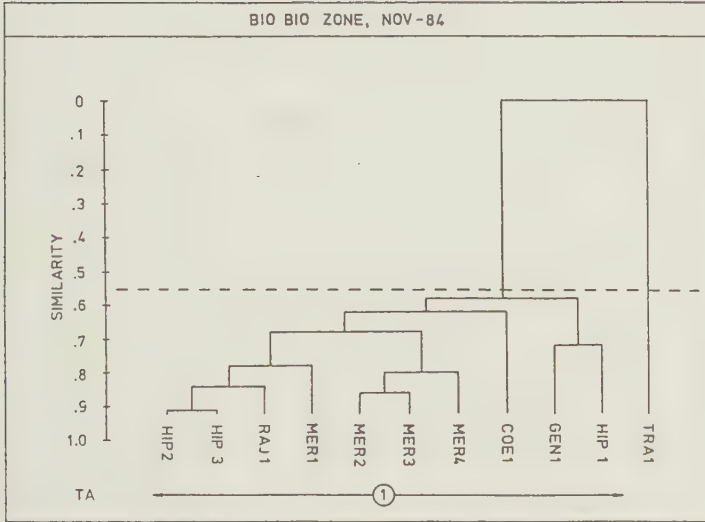


Fig. 18 B. Dendrogram showing classification of predators by size classes in the Bio Bio zone (November 1984; $\alpha = 0.025$) based on wet weight (in percentage) of prey items. The broken line shows the mean level of similarity within size classes of predators. TA = trophic associations. See Table IX for identification of groups.

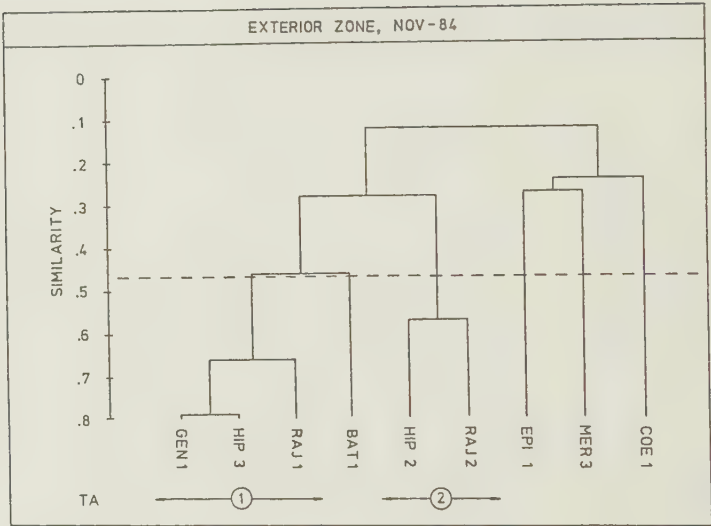


Fig. 18 C. Dendrogram showing classification of predators by size classes in the Exterior zone (November 1984; $\alpha = 0.025$) based on wet weight (in percentage) of prey items. The broken line shows the mean level of similarity within size classes of predators. TA = trophic associations. See Table IX for identification of groups.

3.3.2.3. Exterior Zone.

Significant differences in food of fish within and between groups were found in March and November 1984 (Tables XI a, b; Tables XIV a, b; Figs. 17 C, 18 C). Two major groups can be recognized in both months; all species feed on large crustaceans. *C. aconcagua* is trophically isolated of all groups.

3.3.3. Prey Size Selection.

Frequency distributions of scores ($\text{score} = \ln (w_i/w_j)$) of *M. gayi*, *H. macrops*, *G. maculatus*, *C. aconcagua* and *T. murphyi*, are shown in Figs. 19 A - E. The mean size ratio between predator and prey (by weight) is around 500:1 in *M. gayi*; 200:1 in *H. macrops*; 250:1 in *G. maculatus*; 5,200:1 in *C. aconcagua*; and 16,000:1 in *T. murphyi*. The statistics of scores and sample sizes are given Table XV.

As explained in the last section, the mean of the distribution of score represents the average size relationship between the predator and its prey for all size classes of predator. Feeding selectivity is inversely related to standard deviation of the prey score.

Interspecific comparisons of prey selection reveal a

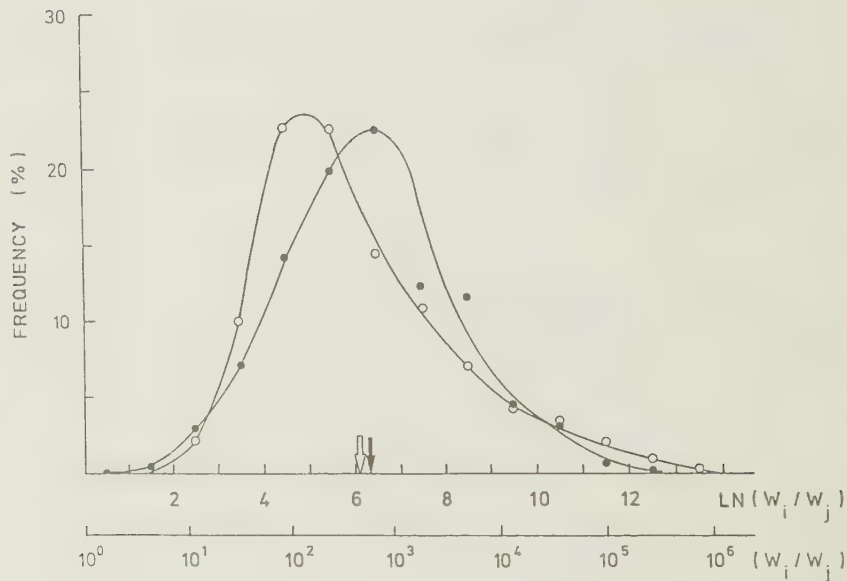


Fig. 19 A. *Merluccius gayi*. Frequency distribution of predator/prey ratio, expressed as $\ln$ (predator weight/prey weight). Dots: March 1984; circles: November 1984. The mean of the distribution is shown by arrow (dark arrow: March; open arrow: November). The curves were eye-fitted.

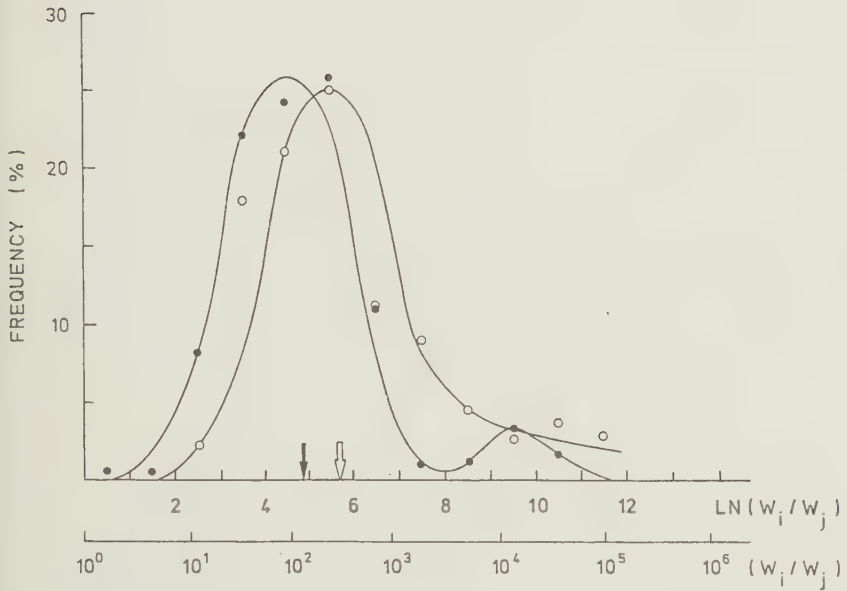


Fig. 19 B. *Hippoglossina macrops*. Frequency distribution of predator/prey ratio, expressed as $\ln$ (predator weight/prey weight). Dots: March 1984; circles: November 1984. The mean of the distribution is shown by arrow (dark arrow: March; open arrow: November). The curves were eye-fitted.

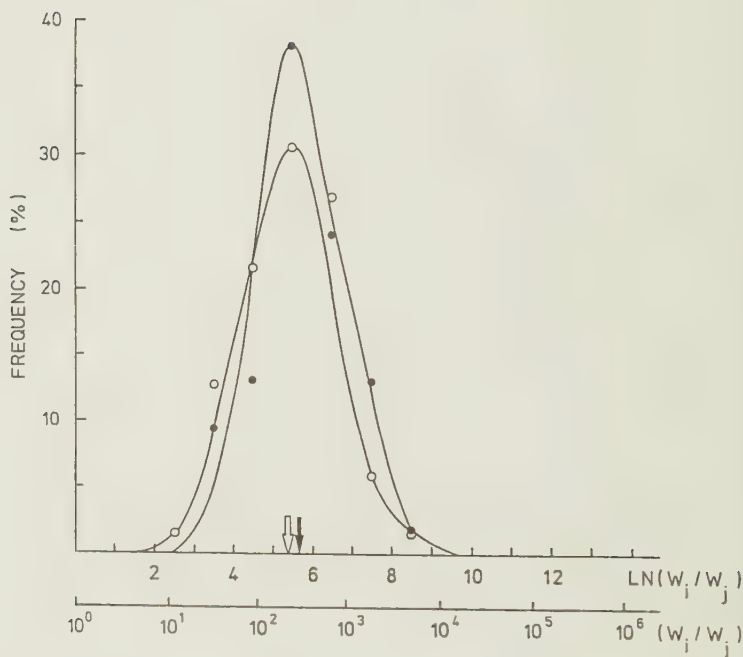


Fig. 19 C. *Genypterus maculatus*. Frequency distribution of predator/prey ratio, expressed as $\ln$ (predator weight/prey weight). Dots: March 1984; circles: November 1984. The mean of the distribution is shown by arrow (dark arrow: March; open arrow: November). The curves were eye-fitted.

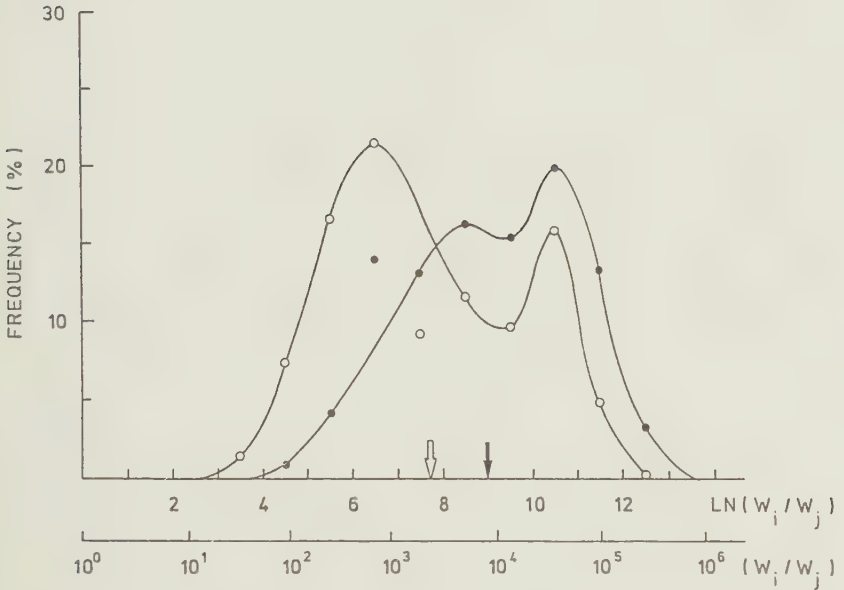


Fig. 19 D. *Coelorinchus aconcagua*. Frequency distribution of predator/prey ratio, expressed as $\ln$ (predator weight/prey weight). Dots: March 1984; circles: November 1984. The mean of the distribution is shown by arrow (dark arrow: March; open arrow: November). The curve was eye-fitted.

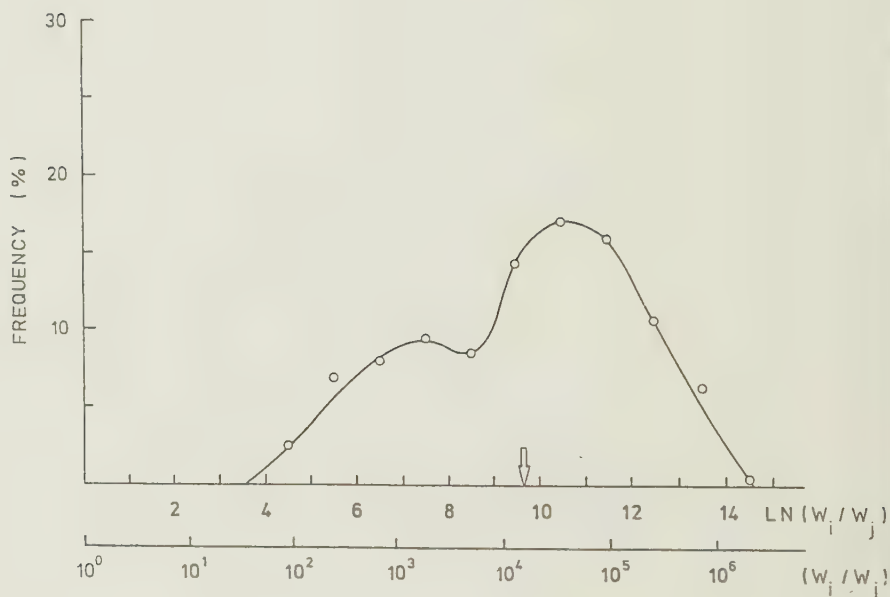


Fig. 19 E. *Trachurus murphyi*. Frequency distribution of predator/prey ratio, expressed as $\ln$ (predator weight/prey weight). Dots: March 1984; circles: November 1984. The mean of the distribution is shown by arrow (dark arrow: March; open arrow: November). The curve was eye-fitted.

considerable degree of separation. For instance, the comparisons by pairs of species within months are all significantly different (t-tests; $p < 0.01$), and each species exhibits a specific average size relationship with its prey. Smaller prey, in relation to the predator weight, are consumed by *C. aconcagua* and *T. murphyi* and larger by *H. macrops* and *G. maculatus*. The widest ranges of prey sizes are shown by the former two species and the narrowest by *G. maculatus*. Comparisons within species between months reveal that the differences are only significant in *H. macrops* and *C. aconcagua* (t-test; $p < 0.01$). The selectivity in all species, with exception of *G. maculatus*, is lower in November than in March.

3.3.4. Ontogenetic Trophic Units.

3.3.4.1. *Merluccius gayi*

Based on ARANCIBIA's (1987) recent report, who found that *M. gayi* undergoes changes in feeding with growth, quantitative analyses were performed with the discriminant analysis (DA) in order to disclose, on a trophic base, the distribution by length groups of predator and to show it in a single picture. All variables used in the analyses

in March and November 1984 passed the tolerance of the F-test ($p < 0.01$); the first two or three canonical discriminant functions were also significant (χ^2 -test; $p < 0.01$) for both months.

In March there is a well defined change in feeding behaviour by size classes (Fig. 20 A; Table XVI a). Sexual immature stages (13-25 cm) are largely planktivorous, feed on Euphausiacea and cannibalize postlarvae. With growth (group 2; 26-35 cm), feeding on Euphausiacea becomes more important but cannibalism is insignificant; pelagic prey as *E. ringens* remains in *Merluccius'* feeding and *P. monodon* does decrease as prey. In group 3 (36-50 cm), *P. monodon* becomes main prey; fish increase and Euphausiacea decrease significantly. Then this heterogenous group enlarges its diet to a mixture of benthic crustaceans and ichthyofagy on both demersal and pelagic fish. The largest group (group 4; 51-66 cm), feeds mainly on crustaceans (*P. monodon* and *P. armata*) but the predation on large pelagic fish as *S. saurus* can become significant in any zones; its feeding heterogeneity is smaller than *Merluccius'* previous group.

Such change in feeding behaviour with growth can also be

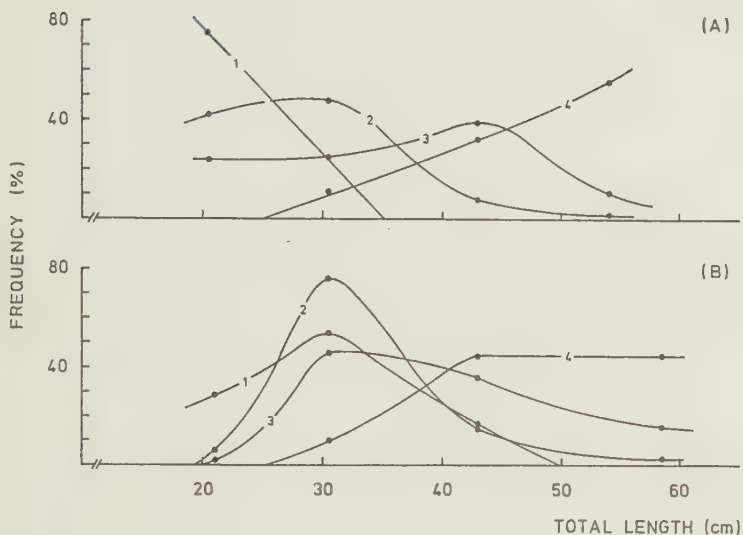


Fig. 20. Frequency distributions of ontogenetic trophic units in *Merluccius gayi* (dots indicate class marks).

A: March 1984 (Actual group key: 1 = 18-25 cm; 2 = 26-35 cm; 3 = 36-50 cm; 4 = 51-57 cm)

B: November 1984 (Actual group key: 1 = 17-25 cm; 2 = 26-35 cm; 3 = 36-50 cm; 4 = 51-66 cm).

recognized in November (Fig. 20 B; Table XVI b) but this progression is not as evident as in March. In group 1, differences in feeding behaviour in relation to March are evident. The predation consisted mainly on *P. monodon* or *Merluccius'* juveniles. Group 2 feeds mainly on *P. monodon* or *E. mucronata* but this group shows also a pelagic/benthic feeding behaviour. Group 3 also feeds mainly on *P. monodon* but the predation on Teleostei is likely reflected in the distribution of its curve; its descendent part is different to the former two groups. Group 4 does remain segregated, being significant main food *P. monodon*, at least more significant than in *Merluccius'* smaller groups. Likely, the segregation of feeding habits per groups is very clear in March due to the feeding resources which are more scarce than in November. This is shown in the apparent "fusion" of the groups 1 and 2. Despite this, *M. gayi* is mainly a pelagic predator in early growth stages and tends to be a benthic/pelagic predator in larger stages.

3.3.4.2. *Hippoglossina macrops*.

All variables used in the discriminant analysis passed the tolerance F-test ($p < 0.01$), and the first two canonical

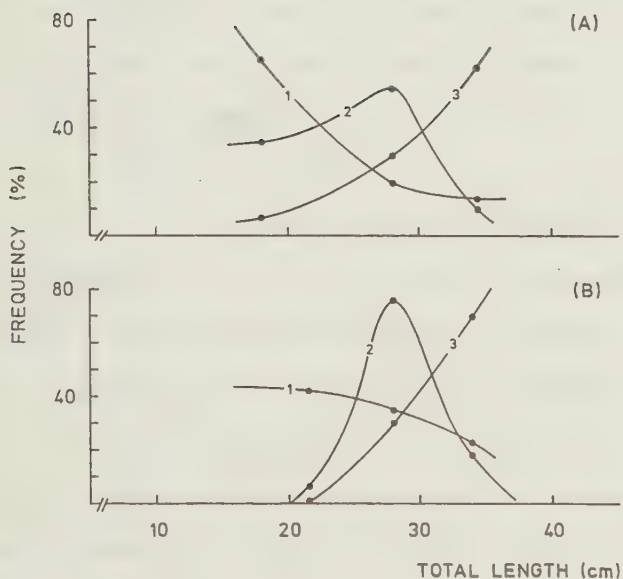


Fig. 21. Frequency distributions of ontogenetic trophic units in *Hippoglossina macrops* (dots indicate class marks).

A: March 1984 (Actual group key: 1 = 10-25 cm; 2 = 26-30 cm; 3 = 31-40 cm)

B: November 1984 (Actual group key: 1 = 18-25 cm; 2 = 26-30 cm; 3 = 31-37 cm).

discriminant functions were significant (χ^2 - test; $p < 0.01$). The food preferences by size classes in March and November are revealed (Figs. 21 A, B; Tables XVII a, b). Although *H. macrops* is mainly a crustacean/benthic predator, there are clear shifts in prey size with growth and, in addition, there is a tendency to stenophagy.

3.3.5. Ontogenetic Ecological Units.

It was previously explained that the weighted overlap index (IND) takes into account the variations of the diet, the distribution of fishes and their abundance. Only a small percentage of analysed pairs of all size classes overlapped at a similarity level greater than 0.25 in the three study zones (Fig. 22). "Important" associations by size groups within each zone are shown in Figs. 23 A - C. The interactions are changing temporally and spatially. The extremely few "important" associations in Achira in relation to the total observations in this zone (6% and 11% in March and November, respectively) are distinguishable. In Bio Bio the number of "important" associations is moderate (24% and 22% in each month, respectively), and in the exterior zone from high to moderate (40% in March; 20% in November).

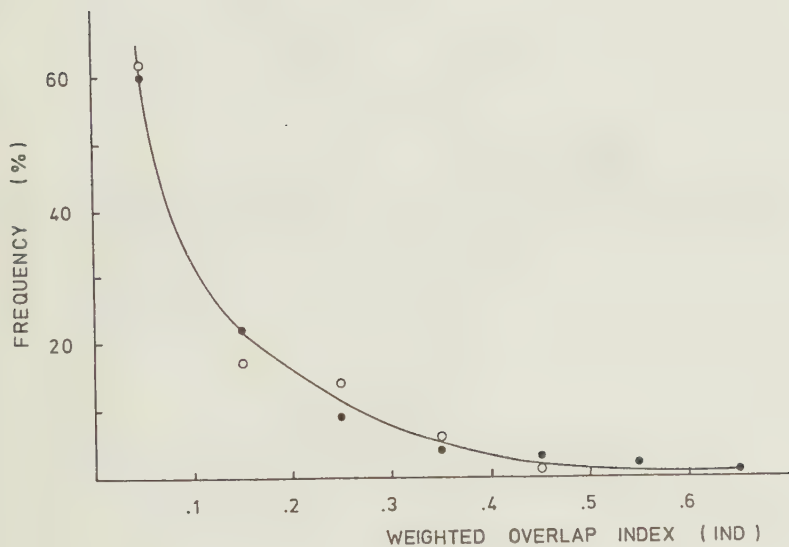


Fig. 22. Frequency distribution of the Weighted Overlap Index values for two surveys ($n = 127$ in March 1984, circles; $n = 124$ in November 1984, dots).

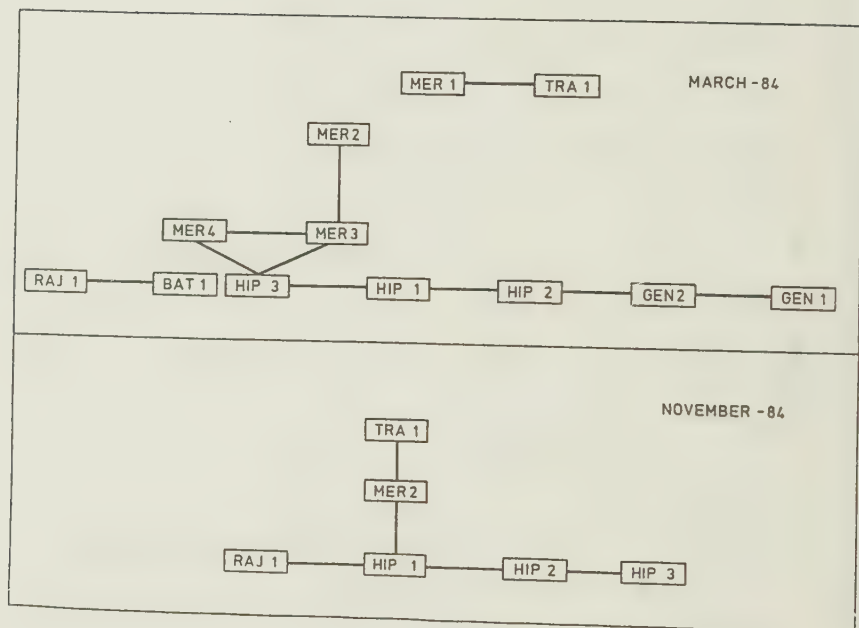


Fig. 23 A. Significant ontogenetic ecological units ($IND > 0.25$) in the Achira zone. The strength of each association is inversely proportional to the length of the line between pairs. The position of the boxes indicate the pelagic or benthic character of fish. Number of pairs analyzed: March = 91; November = 78.

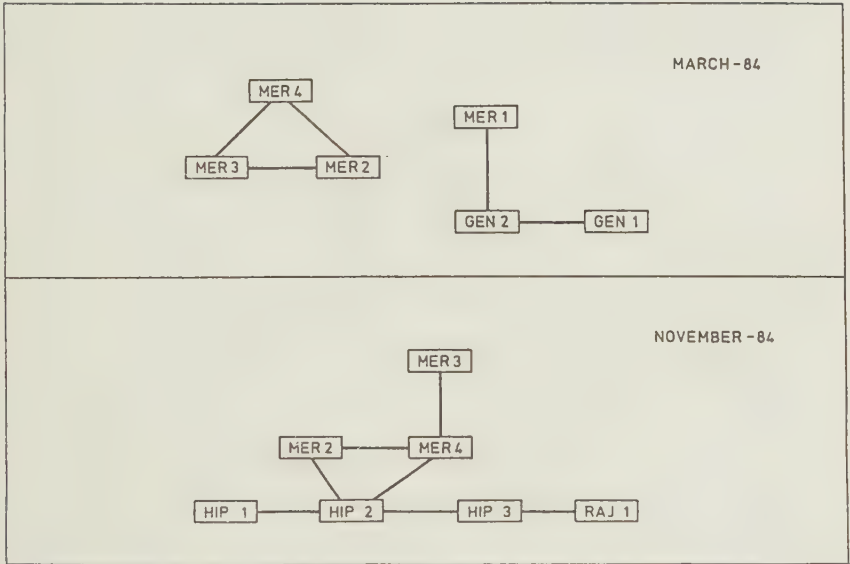


Fig. 23 B. Significant ontogenetic ecological units ($IND \gg 0.25$) in the Bio Bio zone. The strength of each association is inversely proportional to the length of the line between pairs. The position of the boxes indicate the pelagic or benthic character of fish. Number of pairs analyzed: March = 21; November = 36.

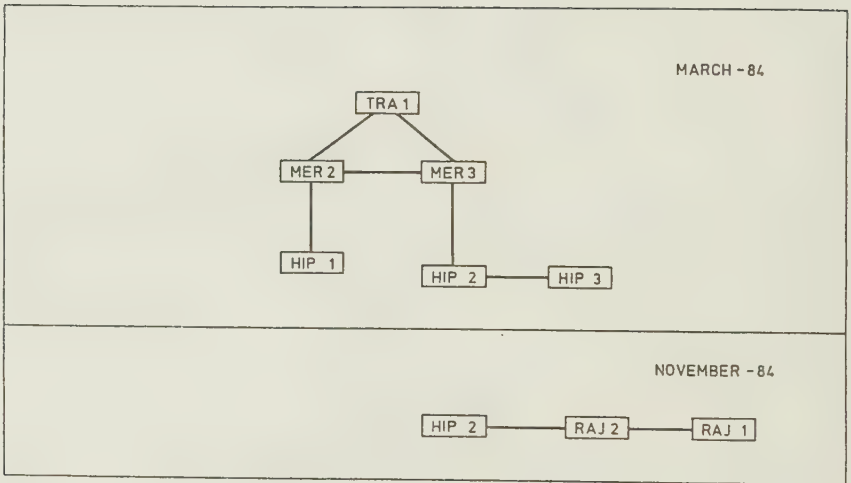


Fig. 23 C. Significant ontogenetic ecological units ($IND \geq 0.25$) in the Exterior zone. The strength of each association is inversely proportional to the length of the line between pairs. The position of the boxes indicate the pelagic or benthic character of fish. Number of pairs analyzed: March = 15; November = 10.

3.4. Discussion and Conclusions.

3.4.1. Feeding Patterns

There are clear evidences that the demersal ichthyofauna divides the food resources among the assemblage members, and several feeding patterns are noticeable. With the exception of *M. gayi* (36-50 cm) and *C. aconcagua* there is a marked tendency toward stenophagy in all species and all their size classes. Moreover, the number of species being "main food" (those items which made up 10% or more of the diet; *sensu* GIBSON and EZZI, 1987) are one or two in pelagic feeders, and commonly two or three in benthic feeders. These results are in accordance with those of GALLARDO *et al.* (1980), for comparable areas (Table XVIII). Their conclusions were, however, erroneous because they, based on lists of trophic spectra, attributed a generalist character to all species of fish in the demersal fish assemblage.

In general, the feeding patterns per species studied in this work are in accordance with species of the same genera. For instance, *T. murphyi* mainly feeds on Euphausiacea or plankton, as reported by ANDRONOV (1983, 1985) for *T. capensis* off Namibia. DAHL and KIRKEGAARD

(1987) reported similar feeding habits for *T. trachurus* off the Danish northwest coast, and KONCHINA (1980, 1983), reported the same for *T. murphyi* off Peru. Recently, MUCK and SANCHEZ (1987) communicated that this species in Peru feeds mainly on Peruvian anchovy (*Engraulis ringens*) in "normal years" and on Euphausiacea during El Niño events.

In *Epigonus* spp., similar feeding patterns have been reported. For instance, MACPHERSON and ROEL (1987) classify *E. telescopus* and *E. denticulatus* off Namibia as pelagic-crustacean feeders, which is partially in agreement with my results for *E. crassicauda*.

Particularly interesting are the feeding patterns of *Merluccius* spp.. All species of this genera undergo similar qualitative and quantitative changes in feeding habits with growth. Mainly, they are crustacean feeders but fish prey in the diet increase as the predator grows larger. Ontogenetic changes in food habits are accompanied by an exponential increase in the mean weight of stomach contents (LIVINGSTON and ALTON, 1982; ANDRONOV, 1983, 1987; DURBIN *et al.*, 1983; SMALE, 1984; GONZALEZ *et al.*, 1985; LIVINGSTON and BAILEY, 1985; ARANCIBIA, 1987; MACPHERSON and ROEL, 1987). Although it could seem trivial, this

must be stressed again because it is frequently forgotten in investigations about food habits of fish, especially when interspecific analyses in a wide length range of predators are done. This characteristic seems to be not so clear in strictly pelagic fish species, at least in Peruvian anchovy (*Engraulis ringens*), Chilean sardine (*Sardinops sagax*) and North Sea sprat (*Sprattus sprattus*), according to my still unpublished data. Seasonal and spatial changes are common in *Merluccius*' food habits (MACPHERSON, 1979; CORDO, 1981; LIVINGSTON, 1983; VINOGRADOV, 1984; ANGELESCU and PRENSKI, 1987). Cannibalism is also characteristic and has been considered as a mechanism regulating the abundance of *Merluccius* (KONCHINA, 1983). PAYNE *et al.* (1987) additionally differentiate between true cannibalism and interspecific predation in two species of *Merluccius* off Namibia. At present, there is also agreement about the opportunistic feeding character of *Merluccius*, which means that despite the relatively high number of prey taxa, only a couple of them must be considered as "main food", since many prey taxa occur only incidentally.

The food resource utilization in strictly demersal fishes,

as flatfish and skates, follows similar patterns as in *Merluccius*. This means that changes in feeding habits with growth can be recognized. Spatial (geographical) and temporal (seasonal) changes in feeding habits are also recognized. In flatfish, this has been reported by ARNTZ (1971, 1978 a, b), ARNTZ and FINGER (1981), MACDONALD and GREEN (1986), LIVINGSTON *et al.* (1986), LIVINGSTON (1987), KNUST (1987), among others. Few exceptions from this rule have been noted. In studies of local, specific areas exceptions probably occur because different species are exploiting abundant food resources (EVANS, 1983; YANG and LIVINGSTON, 1986). ARNTZ (1971), however, argued that diet changes with increasing body size in *Limanda limanda* are less pronounced in regions with a low food supply than in more plentiful areas.

Few scientific studies have been done on the skates in Chile (PEQUENO and LAMILLA, 1985; LEIBLE, 1987), and the information about their feeding habits is very poor. The skates off central Chile are benthic feeders (ARANCIBIA and MELENDEZ, 1987), with crustaceans being the most widely consumed organisms (BAHAMONDE, 1953), similar to *Raja senta* and *R. erinacea* of the east coast of North

America (McEACHRAN *et al*, 1976).

Crustaceans and fish are the main prey in *G. maculatus*. In agreement with MITCHEL (1984) and CLARK (1985 a), who studied the diet of *G. blacodes* off New Zealand, galatheid crustaceans and Brachyura are the main food of small lings. Stenophagy and changes in feeding habits with increasing body size are evident.

References on feeding habits in little demersal sharks are scarce to find, because, like skates, they have no commercial value. Nevertheless and in accordance with this work, SEDBERRY and MUSICK (1978) reported that *Centroscyllium fabricii* in the Middle Atlantic off the USA fed on myctophids and crustaceans.

C. bconcaqua is not of commercial interest (PEQUENO, 1971), and its feeding ecology remains largely unknown. Despite this, high qualitative coincidence in the food of *Coelorinchus* species has been found. McLELLAN (1977) hypothesized that this genus, with long rostrum and small, protusible mouth, is the most extremely specialized form within the macrourids. Polychaetes and small benthic crustaceans are the main food of *Coelorinchus* (OJEDA and

CAMUS, 1977; MACPHERSON, 1979; ARANCIBIA and MELENDEZ, 1987), but CLARK (1985 a) also found fish as prey. *Coelorinchus* is a specialist predator, as is reflected by its prey size; on the other hand, it has a tendency to euryphagy since there is not selection of prey types in a determined range of size.

3.4.2. Resource Partitioning.

TYLER (1972), studying a demersal fish assemblage in temperate waters in terms of food resource division, noted a specialization of the predators due probably to the limitation of food in the system. According to KEAST (1978), seasonal fluctuations of diet overlap between co-occurring species reflect the varying patterns of resource utilization. Additionally, the varying patterns of resource availability affect fluctuations of diet overlap. Besides, as a consequence of the dietary changes with growth, there are often greater interspecific dietary similarities than between size groups of the same species (GIBSON and EZZI, 1987), which is verified by MACPHERSON (1981) and MACPHERSON and ROEL (1987) in demersal fish assemblages of the Mediterranean Sea and off Namibia, respectively. HELFMAN (1978), in an overview about patterns of community

structure in fish, indicates that ontogenetic differences in diet and depth distribution appear to be the rule in fish, which, for instance, was also reported by ARNTZ (1974, 1977) for *Gadus morhua* off western Baltic.

Measures of resource partitioning, as diet overlap or diet similarity, are indicators of coexistence (LANGTON, 1982), because these measures have been observed to decrease rather than increase when resources are limited (ZARET and RAND, 1971). WERNER *et al.* (1977), who studied a freshwater fish community of Michigan, argued that the overlap in the diet of coexisting fish is highest after the spring flush of food and declines when the biomass or density of the food level drops. This seems to be also true for demersal fish assemblages but with a considerable time lag; for instance, in the western Baltic the biomass of macrobenthos, mainly *Diastilys rathkei* and *Nephtys spp.* is more abundant in summer and autumn (ARNTZ, 1978 a). On the other hand, the interrelationships between macrobenthos and demersal fish predators are tight. These macrobenthic taxa are fed upon mainly in summer and autumn. The food overlap of fish in the "benthic summer flush" is higher than in winter and in spring (ARNTZ, 1980).

Several published theoretical points of view about resource partitioning in demersal fish assemblages were verified in this study. First, there are seasonal and geographical variations in diet overlap within the majority, if not all fish species (Figs. 17 A - C and 18 A - C). Second, there can be bigger interspecific dietary similarities than between size groups of the same species. Third, analysing within each zone, the mean diet similarity (Tables XI a, b) in two of three zones studied (Achira and Bio Bio zones) was higher in November (late spring) than in March (beginning of autumn), which could suggest a less limited food resources for late spring/beginning of summer than for autumn/winter.

The mean similarity of diets of demersal fish off central Chile, within each zone of study, is greater in November than in March, as shown in Figs. 17 A and 18 A (Achira zone), Figs. 17 B and 18 B (Bio Bio zone), Figs. 17 C and 18 C (Exterior zone), and Tables XI a, b. Apparently, seasonal changes in food similarity of several demersal fish within zones are due to seasonal availability of food, which seems to be always bigger in the beginning of summer than in autumn. On the other hand, in areas with

prey food largely abundant, the differences in food similarity within and between several groups of fish are not significant, as shown in Fig. 18 B. The demersal fish assemblages exhibit their own mean level of food similarity within zones and seasons, likely as a result of the food abundance.

A great part of the previously referenced literature deals with the research on resource partitioning of demersal fish assemblages in upwelling ecosystems, as it is the case along the coast off central Chile. But, what does occur in demersal coastal assemblages in other temperate ecosystems, for instance, that of the Baltic Sea? Although the demersal ecosystem of the Baltic Sea is a "limited subsystem with a comparatively poor fauna" (ARNTZ 1978 a, b; 1980), the feeding strategies of fish are comparatively the same, i. e. seasonal and spatial changes in the diet composition occur with increasing size of predators, along with considerable inter- and intraspecific differences and low mean overlap values. ARNTZ and FINGER (1981) pointed out that most comparative fish food studies, at least those going into some detail, come to the conclusion that co-existence is probably the most common pattern.

Coincidentally, GROSSMAN (1986), studying a rocky intertidal fish assemblage concluded that food resource partitioning, at least in marine fish (not estuarine), is the most likely process responsible for assemblage organization.

3.4.3. Prey Size Selection

ANDERSEN (1982) developed a hypothesis for feeding with size preferences. According to this hypothesis, prey weight is expected to increase in proportion to predator weight in an environment with equal abundance of prey of all sizes, by logarithmic size classes (URSIN and ARNTZ, 1985 a). In this study, specific prey size preferences were found, but they are not directly comparable with those of URSIN and ARNTZ (1985 b, c), because they used as prey weight the weight of each individual. This seems unrealistic to me because predation on a prey is likely not to be a single predator-prey encounter (CLARK, 1985 b). In fish species that feed on small prey, many fish feed rather on a "bulk prey" and not on an individual. This can be tested, for instance, by looking at the digestion state of prey in predator species. If prey taxa were ingested at the same time, it is obvious that those prey must be found at the same digestion state in the stomach of the predator.

If more than one digestion state are found, each one should be considered a single, independent entity in the ingestion process (URSIN and ARNTZ, 1985 b, c). Just that seems to be the common situation in all demersal fish species studied here, including the specialist fish *C. aconcagua*, and also the pelagic fish *T. murphyi*. However, it should be taken into account that different prey taxa may be digested at different rates. Despite the disagreement with URSIN and ARNTZ (*op. cit.*), it was confirmed that strictly demersal species as *M. gayi*, *H. macrops* and *G. maculatus* show well defined size preferences with log-normal shape.

Pelagic feeders, as *T. murphyi*, and also the specialized benthic feeder *C. aconcagua*, do not show typical log-normal score distributions. Two theoretical explanations can be given: first, the distribution of score is not log-normal in shape when the resources are abundant in nature (URSIN, 1973), or second, the predator feeds without prey size selection on a range of small prey (PLATT and DENMAN, 1978). This second explanation is considered to be more satisfactory to give account of the difference in the observed score distribution in relation to the expected

log-normal shape.

Certainly there are two sources of bias in this type of analysis. First, no attempt to back calculate the observed prey weight in the stomach of predator was made, because the estimated scores are biased rightwards. Second, analyses of score by size classes of predator would be likely to present a different picture (HAHM and LANGTON, 1984), as shown by LIVINGSTON and BAILEY (1985). In this study, previous analyses by size classes of predator did not show significant differences for any species in March 1984 but they were found in *M. gayi* and *H. macrops* in November (t-test; $p < 0.01$).

3.4.4. Ontogenetic Trophic Units (OTUs) and Ontogenetic Ecological Units (OEUs).

LIVINGSTON (1982) pointed out that the availability of food is an important mechanism of segregation in various fish associations, and that past assumptions concerning demersal fishes simply as trophic generalists do not appear to be valid. Many fish exhibit ontogenetic feeding patterns, as has previously been referenced.

As shown in this chapter (section 3.3.4.1.) and, previously, in ARANCIBIA (1987), *M. gayi* exhibits onto-

genetic feeding patterns and undergoes in March a clear shift between two intermediate groups - (26-35 cm) and (36-50 cm) -, corresponding to the size of transition between immature and mature fish, according to the first sexual maturity length (39 cm) reported by BALBONTIN and FISCHER (1981). This physiological process and the shift in feeding habits does not seem to be accidental in fishes. ROSS (1978) reported the same for *Prionotus scitulus*, a Triglidae from Tampa Bay, Florida. Shifts in feeding with growth may exist because intraspecific interactions are avoided (or "competition", *sensu* HELFMAN, 1978; MODDE and ROSS, 1983). The feeding patterns of *H. macrops* confirm an important shift slightly before the onset of reproduction (29 cm TL in females; VOIGTH and BALBONTIN, 1981), and the distribution of OTUs can clearly be recognized in March as in November 1984.

In November, the segregation by OTUs in *M. gayi* is more diffuse than in March. Likely, this difference exists because some food resources are largely available in the sea, being consumed by a large range of length of predator species; as a result, the overlap among predator's size groups becomes higher than in March. Moreover, *P. monodon*

as prey is likely more available in November, especially individuals smaller than 11 mm cephalothorax length. The largest OTU does remain well segregated.

The discriminant analysis (DA) seems to be particularly useful to identify intraspecific groups that change their feeding habits in a continuum, a common situation in demersal fish. Moreover, each fish can be "objectively" classified by DA, which yield, as a result, less artificial groups than those yielded by the investigator's subjectivity. A disadvantage of DA seems to be, for all not experienced people, the interpretation of the output, including the relationships between variables and canonical variables. Furthermore, I thought it unnecessary to go into details for descriptions of prey by groups, which has previously been done.

In order to analyse intra- and interspecific size classes the diet and the distribution and abundance of predators were taken simultaneously into account. The concept of ontogenetic ecological unit (OEU) is now available (MACPHERSON and ROEL, 1987). My results about OEUs are very similar to those of these authors, for comparable upwelling ecosystems (southeast Pacific Ocean and south-

east Atlantic Ocean, respectively). Only a small percentage of all size classes considered overlap at a similarity level greater than 0.25 (Fig. 22), and the frequency distributions of the Weighted Overlap Index (IND) in both investigations are very similar. The similarity between OEUs indicates that the community studied is highly differentiated and that interactions are weak.

The advantage of IND is evident; it takes into account diet and distribution of predators, which lack in the similarity indices. An interesting area of work seems to be to investigate the distribution of IND in order to test the level of significance of the OEUs.

This work, theoretically supported with relatively old ideas about modelling of ecosystems taking into account trophic linkages (ANDERSEN and URSIN, 1977) and approaches with more advanced ideas (LIVINGSTON, 1982; MACPHERSON and ROEL, 1987) reveals several common patterns in different demersal fish assemblages. Consequently, in the future, fish assemblages off central Chile should be modelled under clear conceptual and practical approaches.

4. CONSUMPTION OF *Pleuroncodes monodon* BY *Merluccius gayi* AND *Hippoglossina macrops* IN CENTRAL CHILE.

4.1. Introduction.

With the increasing importance of multispecies management it is essential to understand the role of fish predators within the ecosystem (MAJKOWSKI and WAIWOOD, 1981; CADDY, 1985; LIVINGSTON, 1985; MACPHERSON, 1985 a). As a part of this, it is necessary to determine the feeding habits and the daily ration of the major species (HUEBNER and LANGTON, 1982; DURBIN *et al.*, 1983).

WOROBEC (1984) pointed out that the quantification of food consumed by abundant fish species is an important area of study in marine trophodynamics, and the effect on exploited populations and ecosystems, as a whole, is currently one of the main objectives of fishery research (MACPHERSON, 1983, 1985 b; LLEONART *et al.*, 1985 a, b); ROEL and MACPHERSON, 1988).

As I have shown in the previous chapters, *M. gayi* and *H. macrops* play an important role as predators of *P. monodon* in central Chile. Besides, these three species form the basis of the commercial trawl fisheries. Thus, the

predatory impact of both fish species on *P. monodon* is of considerable interest. At present, no quantitative information on consumption of fisheries resources has been carried out in central Chile, except by ARANCIBIA *et al.* (1986), who estimated the predation mortality of *P. monodon* by *M. gayi*.

Consequently, the purposes of this chapter are to estimate the daily ration of *M. gayi* and *H. macrops*, in particular on *P. monodon*, and to estimate the consumption of this crustacean by both fish species.

4.2. Materials and Methods.

4.2.1. Sampling.

Details of sampling and analyses of stomach contents in the laboratory were given in chapter 3 (pages 62 - 63). Weight of individual fish was estimated using published length-weight relationships per sex (AVILES *et al.*, 1979; VOIGTH and BALBONTIN, 1981).

Only ingested specimens of *P. monodon* where the cephalothorax length (CL, in mm) could be measured were considered in the analysis. Their original weight were back-calculated using published length-weight relationships per sex (IFOP, 1980). When it was not possible to measure CL due to a very advanced digestion state of the prey, the predator and its prey were discarded. With this procedure, only few samples had to be discarded because, even in advanced digestion states, CL is relatively easy to measure by putting the cephalothorax into water.

4.2.2. Instantaneous Coefficient of Gastric Evacuation, Digestion Time, Daily Ration and Mean Initial Prey Weight.

Evacuation of prey from fish stomachs is described by an

exponential function, independent of fish size (SWENSON and SMITH, 1973; ELLIOTT and PERSSON, 1978; GROVE *et al.*, 1978; HUEBNER and LANGTON, 1982; WOROBEK, 1984) but if fish are trophically inactive after ingesting prey, as seems to be the case with *M. gayi* and *H. macrops*, digestion of such prey can be described by the equation

$$S_t = S_o \cdot e^{-(R \cdot DT)} \quad \dots (1),$$

where S_t = food weight at end of digestion period (arbitrarily considered to be 2% of its initial weight); S_o = initial weight of prey; R = instantaneous coefficient of gastric evacuation; DT = digestion time (ELLIOTT and PERSSON, *op. cit.*; MACDONALD *et al.*, 1982; WOROBEK, *op. cit.*).

According to JONES and GEEN (1977) and DIANA (1979), in this type of predation, the most appropriate equation for calculating daily ration is

$$DR = \frac{\bar{W} \cdot N_f}{DT \cdot N_t} \quad \dots (2),$$

where DR = daily ration (in g or % of wet body weight, %BW); $\bar{W}$ = mean initial weight of prey (in g or %BW); N_t =

number of stomachs sampled; N_f = number of full stomachs; DT = digestion time for prey items in days, as estimated from equation (1). $\bar{W}$ was calculated per OTUs in *M. gayi* because the per hour sample size was considered enough, but because the sample size was smaller in *H. macrops*, $\bar{W}$ was assumed to be equal in each OTU.

As Chile's "normal local time" is yearly changed to "summer time" from October to the beginning of March, the former was used in this study in order to make the samples of March and November on an hourly basis comparable.

The instantaneous coefficient of gastric evacuation (R , h^{-1}) was estimated according to WOROBEK (1984), who found, from experimental data, a linear relation between R and temperature (T , $^{\circ}C$) for fish feeding on small prey (polychaetes, small crustaceans). The equation for the calculation of R is

$$R = - 0.0442 + 0.0175 T \quad (r^2=0.62; d.f.=34) \dots (3).$$

The mean initial weight of prey (in this case only *P. monodon* as percentage of predator body weight) was estimated hourly and the great mean was calculated, which finally is the $\bar{W}$ value per OTU. Since only diurnal

trawls were performed, it was assumed that W_i (i = hour, from 19 to 6) is equal to the great mean, for hourly data between 7 and 18 h. The water temperature was obtained from data of the Instituto Hidrográfico de la Armada de Chile (Navy Hydrographic Institute).

4.2.3. Population Consumption.

Population consumption estimates on a monthly basis were calculated using the formula reported by LIVINGSTON *et al.* (1986), modified from MEHL and WESTGARD (1983). This equation is

$$C_{ijk} = DR_{ij} * D_i * B_j * P_{ijk} \quad \dots (4),$$

where C_{ijk} = consumption of prey k by predator j during season (or month) i ; DR_{ij} = daily ration (%BW), as the fraction of body weight consumed per day of predator j in season (or month) i ; D_i = number of days in season (or month) i (in this study is a constant term equal to 30); B_j = biomass of predator j ; and P_{ijk} = proportion (by weight) of prey k consumed by predator j in season (or month) i (in this study is a constant term equal to 1 because only *P. monodon* as prey is considered). Then, equation (4) is reduced to

$$C_{ij} = DR_{ij} * B_j * 30 \quad \dots (5).$$

The consumption within each fish species was estimated by taking the ontogenetic trophic units (OTUs) into account, as defined in the previous chapter. Then, equation (5) has the final form

$$C_{ijl} = \sum_{l=1}^n (DR_{ijl} * B_{jl} * 30) \quad \dots (6),$$

where the terms are as defined in (5) but taking into account the subindex l = ontogenetic trophic units, from 1 to n .

4.2.4. Predator Biomass.

The standing stock of *M. gayi* and *H. macrops* in the area of study in March 1984 has been reported by BAHAMONDE *et al.* (1984). Since specimens of *M. gayi* smaller than 25 cm TL do not feed much on *P. monodon*, they were discarded from the following analyses. The biomass per OTU was estimated according to the proportional distribution of biomass by age in the stock, independently by males and females, according to AGUAYO and ROBOTHAM (1984). It was assumed that the biomass of *M. gayi*, per age, in March and November 1984 had the same distribution as in 1982. This

assumption is sensible because the stock of *M. gayi* in Chile has remained in the same level since 1973 (AGUAYO and ROBOTHAM *op. cit.*). Age at length was estimated for *M. gayi* using equations reported by AVILES *et al.* (1979). For *H. macrops* there is no age/length relationship available. The biomass of *H. macrops* per OTU was estimated with the assumption that the weight distribution by lengths in the stock was proportional to the weight distribution in the random samples, because the catch was not completely counted but completely weighted.

Estimations of the standing stock of both *M. gayi* and *H. macrops* in November 1984 have not been reported by official Chilean institutions. Hence, I derived them from raw data following PALOHEIMO and DICKIE (1964) and ALVERSON and PEREYRA (1969), according to the equation

$$B_i = \frac{A_j}{\bar{a} * c} * \overline{cpue}_j \quad \dots (7),$$

where B_i = biomass of species i ; A_j = area of investigation, in km^2 ; $\bar{a}$ = mean trawling area, in "lineal-km" (constant term equal to $0.0174 km^2$; ANONYMOUS, 1984 a); $\overline{cpue}_j$ = mean catch per unit of effort by zone, in kg; c =

proportional coefficient relating to the efficiency of the fishing gear (PALOHEIMO and DICKIE, *op. cit.*). In this study "c" is a constant term equal to 1 because both the research vessel and the fishing gear were the same.

The biomass per OTU in November 1984 was subsequently estimated following the same assumptions as in March 1984. OTUs per species used in this analysis, as shown in chapter 3, are

Merluccius gayi (Chilean hake)

OTU	LENGTH RANGE (TL, in cm)	AGE (years)
2	26 - 35	3
3	36 - 50	4,5,6
4	> 51	> 7

Hippoglossina macrops (bigeye flounder)

OTU	LENGTH RANGE (TL, in cm)
1	10 - 25
2	26 - 30
3	> 31

4.3. Results.

4.3.1. *Merluccius gayi*

Individuals of this species seem to be trophically inactive after ingesting prey, because the percentage of stomachs containing only one taxon reached 77% in March and 60% in November. If more than one prey portion (usually consisting of individuals of one species) has been predated, commonly the other has an advanced digestion state. This confirms that individuals of *M. gayi* remain trophically inactive for some time after feeding. This trophic behaviour suggests that the use of DIANA's model (1979; cf. equation 2, page 116) is the most appropriate for estimating the daily ration. Particularly interesting is the diurnal feeding behaviour of *M. gayi* on *P. monodon* (Fig. 24; Tables XIX a, b), with the predation peak between 14-17 hours in March and 13-16 hours in November.

The estimated values of the initial mean weight of ingested food ($\bar{W}$), daily ration (DR), predator biomass (B) and consumption of *P. monodon* by *M. gayi* (C) are given in Tables XX a, b. In March 1984, C reached 42.2 t and 213.5 t in November.

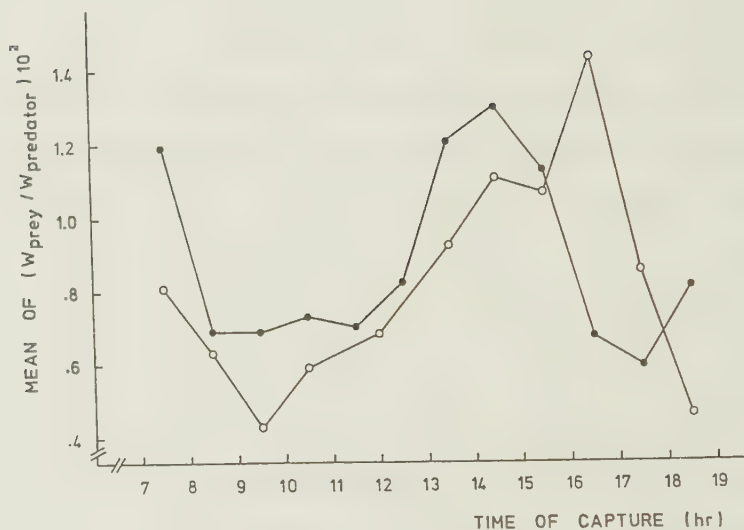


Fig. 24. *Merluccius gayi*. Daylight variation in the *P. monodon* weight/fish weight ratio at time of capture. Curve smoothed using the moving average by twos to clarify trend. Circles: March 1984; dots: November, 1984.

4.3.2. *Hippoglossina macrops*

As with *M. gayi*, individuals of this species seem to be also trophically inactive after ingesting prey, because the percentage of stomachs containing only one taxon reached 88% in March and 84% in November. Unlike *M. gayi*, *H. macrops* seems to feed on *P. monodon* without day-time preference (Fig. 25; Tables XXI a, b). The estimated values of $\bar{W}$, DR, B and C are given in Tables XXII a, b. In March 1984, C reached 627.6 t and 93.6 t in November.

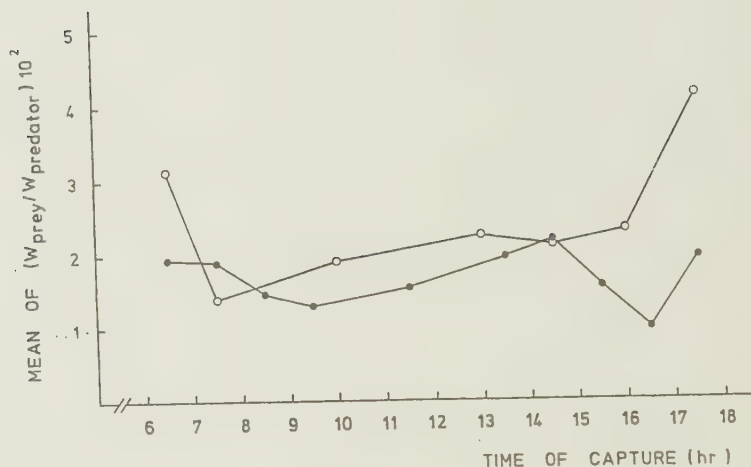


Fig. 25. *Hippoglossina macrops*. Daylight variation in the *P. monodon* weight/fish weight ratio at time of capture. Curve smoothed using the moving average by twos to clarify trend. Circles: March 1984; dots: November 1984.

4.4. Discussion and Conclusions.

The equation of DIANA (1979) considerably simplifies the calculations and methods to ascertain the daily ration (DR) for the studied fish, as has also been reported by MACPHERSON (1985 a) for some demersal fish off Namibia. My data seem to be adequate for the estimation of DR in *M. gayi*, with *P. monodon* as prey, because this fish species exhibits a diurnal period of highest predation activity on this crustacean (Fig. 24). Apparently, this period has been well sampled and, consequently, the bias in DR reduced. Unlike *M. gayi*, *H. macrops* does not exhibit a period of highest predation activity in the diurnal time (Fig. 25). Presumably, the sampling could not be satisfactory to estimate DR for *H. macrops* and the bias could be significant.

Other source of bias in the estimation of DR could be the initial prey weight value ($\bar{W}$), which was assumed to be equal to the mean of several hours (diurnal time). Likely, as suggested by several authors, the stomach sampling to estimate $\bar{W}$ must be performed each 3 hours along a day, at least for fish species that do not exhibit a predation peak on *P. monodon*, as *H. macrops*. In *M.*

gayi it seems sensible to sample stomachs at afternoon but a decision must be reached after a 24 hours-sampling study.

In order to reduce the bias in the estimation of DR, it is also necessary to perform experimental investigations to estimate digestion time (DT). Likewise, it is necessary to provide experimental data of the instantaneous coefficient of gastric evacuation (R) because it tends to be scarce for demersal fish (MACPHERSON, 1985 a). Nevertheless, intensive field sampling to calculate the number of full stomachs (N_f) and the number of stomachs sampled (N_t) is likely to reduce the sources of error more effectively than the error in R (TYLER, 1970; JONES, 1974; COCHRAN and ADELMAN, 1982; WOROBEK, 1984).

The accurately identification of intraspecific size groups with similar feeding habits, in this work named ontogenetic trophic units, can help us to reduce considerably the data matrices used to estimate the predation mortality. At present, this type of matrices consider the predator (by age) and their prey (by age), therefore the required information is enormous and, many times, difficult to obtain. This strategy of analysis, i.e. taking into account changes in food composition by predator size

groups, would be an important consideration in future management analyses incorporating predation mortality, as part of natural mortality, into classical fisheries models (CADDY, 1985). In this work, assuming that the estimated consumption values of both fish species (Tables XX a, b and XXII a, b) are representative within each semester (autumn-winter and spring-summer) and that the mean biomass of the stock of *P. monodon* in 1984 was 32,149 t (average between March, 35,940 t, and November, 28,358 t), it can be concluded that *M. gayi* and *H. macrops* jointly removed in 1984 a biomass value of *P. monodon* equivalent to 18% of the estimated standing stock.

Probably *M. gayi* is the major consumer in the food web off central Chile. Other species of *Merluccius* play a similar role in comparable ecosystems (DURBIN *et al.*, 1983; REXSTAD and PIKITCH, 1986; PAYNE *et al.*, 1987). Through analysis of predation on *P. monodon*, *H. macrops* must also be considered as an important predator. Seasonal variations in consumption of *P. monodon* by fish are evident, therefore caution must be taken with this type of variation if population consumption are performed (SMAGULA and ADELMAN, 1982). The analysis must likely be reduced to

a seasonal basis.

Despite this, it is evident that *P. monodon* suffers an extremely high predation mortality, primarily by *M. gayi* and *H. macrops*, and perhaps secondarily by *Genypterus maculatus*, as suggested by HENRIQUEZ and BAHAMONDE (1964) and BAHAMONDE and ZAVALA (1981). Moreover, size-specific and seasonal predation on this crustacean are evident, as shown in Figs. 26, 27 and 28. Juveniles are heavily predated by *M. gayi* and *H. macrops*, and larger specimens by *G. maculatus*. This confirms previous reports for other major predators, where the predation pressure is higher on young individuals of the prey (LLEONART *et al.*, 1985 a, b; EUZEN, 1987; MAGNUSSON and PALSSON, 1987; PAYNE *et al.*, 1987). ARANCIBIA *et al.* (1986) reported for *P. monodon* smaller than 11 mm cephalothorax length (year class 0) a predation mortality equal to 2.478, taking only *M. gayi* as predator into account; for classes 1+, they reported an "average" predation mortality equal to 0.008.

At present, the incorporation of fish feeding habits into fisheries assessment models are fashionable because the main links among species in the models are submodels describing diet composition and food intake (LIVINGSTON,

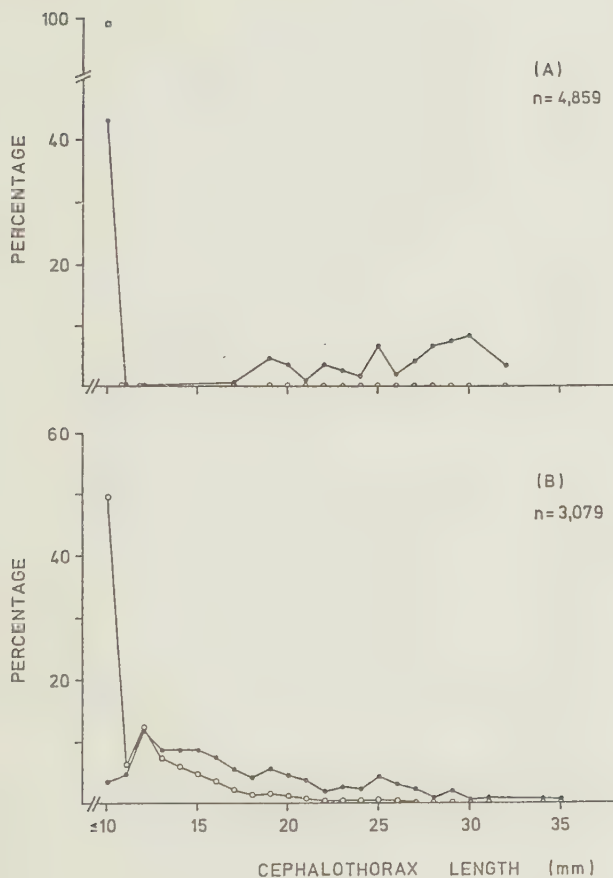


Fig. 26. Frequency distribution of abundance (circles) and weight distribution (dots) by length of *P. monodon* ingested by *M. gayi*.

A: March 1984; B: November 1984

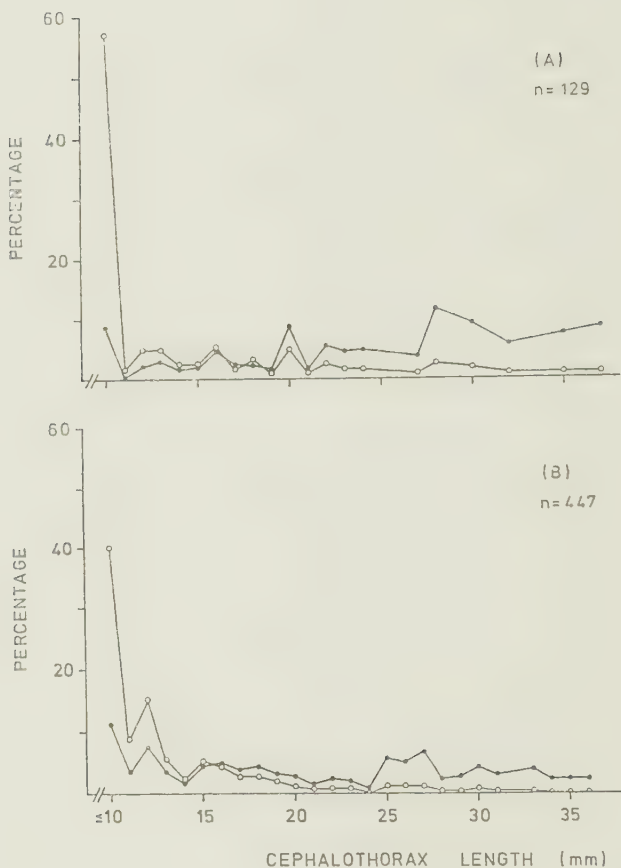


Fig. 27. Frequency distribution of abundance (circles) and weight distribution (dots) by length of *P. monodon* ingested by *H. macrops*.

A: March 1984; B: November 1984



Fig. 28. Frequency distribution of abundance (circles) and weight distribution (dots) by length of *P. monodon* ingested by *G. maculatus*.

A: March 1984; B: November 1984

1986). Interesting guides to model the interaction of *P. monodon*, their natural predators, and their fisheries are given by BRANDER and BENNET (1986), who studied the interactions among Norway lobster (*Nephrops norvegicus*), cod (*Gadus morhua*), and their fisheries; and by HOPKINS (1987), who studied the mortality of the deep-water prawn (*Pandalus borealis*).

I think that the multispecies assessment, following the recommendations of the International Council for the Exploration of the Sea (GISLASON and SPARRE, 1985, 1987), will not soon be performed in Chile because quantitative data of predation in commercial fish species are very scanty and, foremost, it will be necessary to develop a "Stomach Sampling Project" following ANONYMOUS (1984 b). I consider that studies about predation mortality and, consequently, multispecies analyses in fisheries biology are not impossible to be conducted in the near future in Chile because the private fishery can support them. I think that the main problem is to remove the Chilean managers' lethargy, who, at present, continue their analyses with old monospecific approximations. It will be also necessary to sample, on a monthly or seasonal basis,

the prey - *P. monodon* - and its more important predators - primarily *M. gayi*, *H. macrops* and *G. maculatus* -, in order to estimate not only the biomass of each one but also their productions. Both parameters are considerable useful in fisheries biology but the idea is to reach the capacity to make multispecific analyses, which has been demonstrated to be more realistic than old, and many times, unadequate monospecific approaches.

5. SUMMARY AND CONCLUSIONS

This thesis deals with the distribution of the ichthyofauna in the area of the fishery of *Pleuroncodes monodon* (*Galatheidæ: Anomura*), their trophic relationships, and the interactions among the stocks of the demersal fish *Merluccius gayi* and *Hippoglossina macrops*, and *P. monodon*.

The study area is located between 35°45' S - 37°10' S, on the continental shelf and on the upper slope off central Chile. The data was obtained during four bottom trawl surveys carried out in April 1982, April 1983, and March and November 1984.

Fish pattern distribution

Two ichthyofaunal boundaries (at 100 m and 250 ± 50 m depth) and three assemblages (inshore on the continental shelf, offshore on the continental shelf, and on the upper slope) were found. Inshore *M. gayi* is the most abundant species in association with pelagic and/or coastal fish (e.g. *Trachurus murphyi* and *Prolatilus jugularis*, respectively); offshore *M. gayi* is also the most abundant species but in association with *Hippoglossina macrops*; on the upper slope *Coelorinchus aconcaagua* progressively

replaces *M. gayi*, in association with the bathypelagic fish *Epigonus crassicauda*, skates and sharks.

All assemblages exhibit low values of biomass heterogeneity and high values of dominance. Frequently, only 3 or 4 fish species, and often only 1 or 2, constitute more than 80% of the catch, independent of the season.

The ichthyofaunal boundary at 250 ± 50 m depth coincides with the presence of the Günther Current - formed by equatorial subsuperficial waters - and, partially, with the edge of the continental shelf. The biggest concentrations of *M. gayi* are found at and near this boundary suggesting that oxygen deficiency in the Günther Current is not a limiting factor for this species.

Temporal (seasonal), geographical and bathymetric fluctuations in demersal fish distribution patterns appear to be common in the study zones and are probably correlated with changes in the substrate and in the abiotic parameters of the water column. The deepest boundary coincides with the edge of the continental shelf and the presence of the Günther Current. The fish assemblage is displaced ca. 50 m upwards and towards the

coast in spring/summer in contrast to autumn/winter, which is likely to be correlated with, and synchronized to, the displacement of the anticyclonic center over the southeastern Pacific Ocean which influences the movements of the water masses in the region. A clear example of this interaction is increased upwelling in spring/summer when equatorial subsuperficial waters flow near and at the surface.

The problem concerning the cluster analysis and the significance of the difference of a similarity index between and within entities has also been taken into account by using the Mann-Whitney U-test. Several examples using fish catch data have demonstrated that this approach is reasonable.

Trophic relationships.

The feeding patterns in the investigated fish species reveal clear tendencies toward stenophagy. Significant exceptions to this rule are *C. biconcava* and the size class 36-50 cm TL in *M. gayi*. This stenophagous character is revealed by both low values of feeding heterogeneity and low number of prey taxa contributing significantly to the food, commonly 1 or 2 in pelagic-feeding fish species,

and 2, 3 or a maximum of 4 in benthic-feeding fish species. Spatial, temporal and size-specific changes in feeding behaviour seem to be the rule in the studied demersal fish species.

M. gayi, the most abundant fish species, exhibits changes in food habits with growth. It is mainly a crustacean-feeder with an increasing proportion of fish prey with increasing growth. Furthermore, the weight of the stomach contents increases exponentially with the size (by length) of the predator. Although cannibalism was also observed, it can not be concluded that this behaviour plays a significant role in regulating *Merluccius'* abundance.

The division of food resources between and within species seems to be a very important mechanism operating in the demersal fish assemblage that favours the co-existence of predators. Several patterns of resource partitioning have been verified in this study. For instance, seasonal variations in the diet overlap of co-occurring species are rather the rule, due likely to the seasonal availability of prey. The trophic associations are dynamic within and between zones, confirming non-stable entities in both seasonal and geographic terms. Intraspecific trophic

overlap seems to be avoided by use of different prey taxa, or by specific prey selectivity in terms of a differential predation pressure based on the length of prey. These results in interspecific dietary similarities are often greater than intraspecific ones.

Prey size selection seems to be an important mechanism to permit the co-existence of fish predators. Several fish species feed on prey with a specific "score distribution" ($\text{score} = \ln(\text{predator weight/prey weight})$). Many predators exhibit typical score distributions with their own parameters. Interspecific differences are often significant. Demersal fish species feeding on a relatively wide range of prey size, as *H. macrops*, *M. gayi* and *G. maculatus*, show a log-normal distribution of score; the curves are typically platykurtic in the former species, leptokurtic in the last and intermediate in *M. gayi*. Fish species feeding on a narrow prey size do not show an approximate log-normal distribution of score, e.g. the demersal fish *C. aconcagua* and the pelagic fish *T. murphyi*.

Ontogenetic feeding patterns also are a common pattern in demersal fish. Two species analysed in this study, *M. gayi* and *H. macrops*, exhibit a shift slightly before the

onset of reproduction. Pelagic and benthic feeders are well identified using the conceptual approach of ontogenetic trophic units (OTUs), where large size groups including several annual classes form clear groups. Of course, these entities are rather a continuum but they can be identified by using multivariate techniques such as the discriminant analysis, which is not possible to perform with a combination of artificial groups, for instance, groups of 5 or 10 cm total length subjectively displayed by the investigator. The OTUs also seem to be non-stable entities, at least in intermediate groups, with higher overlap in a "spring/summer situation" than in an "autumn/winter situation".

Feeding behaviour is probably very important in avoiding intraspecific interactions (or "competition", *sensu* ARNTZ and FINGER, 1981), as revealed by OTUs. However, the distribution and abundance of predators can also be important mechanisms of avoiding intra and interspecific interactions (*ibid*, *op. cit.*). The modern concept of ontogenetic ecological units (OEU) becomes a tool to reduce and to integrate information in order to analyse and to describe interactions among fish entities in the community.

The use of OEUs allowed us to conclude that "significant" associations by size groups are rather scarce, which means that the community studied is highly differentiated. This could mean that trophic resources are not widely available, and that the mechanisms of segregation are efficient.

Consumption of *P. monodon* by *M. gayi* and *H. macrops*.

Several parameters must be taken into account to calculate the consumption of *P. monodon* by *M. gayi* and *H. macrops*. Despite this, it is necessary to investigate this field of fisheries biology because it can help us to understand the interactions among stocks and the fisheries.

During March 1984, the daily ration (DR) of *P. monodon* as prey showed a clear tendency to decrease in *M. gayi* as the fish grows, but in November 1984 a relatively constant pattern emerged. In *H. macrops*, DR increases as the predator grows.

In order to reduce the bias in the estimations of DR, it is recommended to increase the sample size on an hourly basis during a 24 hours period. This will allow us to test, by refuting or confirming, the daily trend in predation of *P. monodon* by demersal fish. In this study,

clear diurnal variations are shown in predation of *P. monodon* by *M. gayi*, which occurs principally between 13 and 17 hours in March, and between 12 and 16 hours in November. Unlike *M. gayi*, *H. macrops* does not show a diurnal trend in predation of *P. monodon*. The data used to estimate DR in *M. gayi* seems to be adequate because its period of highest predation activity on *P. monodon* has largely been sampled. But the data were not sufficient in *H. macrops*. Consequently, the bias in DR was found to be low in *M. gayi* but significant in *H. macrops*.

The identification of intraspecific size groups with similar feeding habits (ontogenetic trophic units, OTUs) can become a useful tool for estimations of predation mortality in other fishery resources. The classical data matrices used in multispecies analysis to estimate predation mortality can largely be reduced by using OTUs because these entities are conformed by several year classes of predator.

In this work, the consumption of *P. monodon* by *M. gayi* and *H. macrops* was estimated by using OTUs. These results (Tables XX a, b and XXII a, b) together with two assumptions (first, that the estimated consumption values

of both fish species in March and November 1984 are representative within each semester - autumn/winter and spring/summer, respectively - and, second, that the standing stock of *P. monodon* in 1984 was 32,149 t, which corresponds to the average between March, 35,940 t, and November, 28,358 t) allow us to conclude that in 1984 both fish species jointly removed a biomass value of *P. monodon* equivalent to 18% (5,787 t) of the estimated standing stock. It must be stressed that the fishery on *P. monodon* collapsed long ago and, at present, the annual fishing quota (4,400 t) is harvested in one week.

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Table I. "*Pleuroncodes monodon* surveys" carried out on the continental shelf and on the upper slope off central Chile from 1982 to 1984.

Year	Area intervals	Depth range (m)	Period
1982	35°47' S 37°05' S	42-300	April 4-30
1983	35°50' S 37°01' S	52-350	April 15- May 8
1984 a	35°45' S 37°10' S	40-355	March 14- April 4
1984 b	36°00' S 36°55' S	33-300	Novem- 4-23 ber

Table II. Depth range used in this study
(see text for explanations).

Depth range (m)	Symbols
≤ 100	1
101 - 150	2
151 - 200	3
201 - 250	4
251 - 300	5
> 301	6

Table III. Number of samples (bottom trawl hauls) per survey and zone. Numbers in brackets: number of species contributing $> 1\%$ to the biomass.

Survey	Achira (= A)	Bio Bio (= B)	Exterior (= E)
April 82	83(11)	51(3)	23(5)
April 83	79(9)	43(7)	21(5)
March 84	70(7)	41(4)	25(6)
Nov. 84	74(8)	49(8)	13(7)

Table IV. Percent contribution of biomass of the most important fish species caught in surveys for *P. monodon* on the continental shelf and on the upper slope off central Chile in 1982, 1983 and 1984 (March and November).

Species	1982, April	1983, April	1984, March	1984, Nov.
<i>Merluccius gayi</i>	74	82	33	54
<i>Hippoglossina macrops</i>	2	6	52	13
<i>Coelorinchus aconcagua</i>	7	2	7	13
<i>Genypterus maculatus</i>	4	2	2	3
<i>Trachurus murphyi</i>	13	5	2	3
<i>Prolatilus jugularis</i>		1		5
Elasmobranchii (skates and little sharks)	1	1	4	8

Table V a. Range of community parameters per survey.
Zone A: Achira. Key: S = species number; C =
mean capture/trawl (kg); H' = diversity; J =
evenness (the depth strata as shown in Table
II).

Survey		S	C	H'	J
April	1982	3 - 7	75-276	0.8-1.5	0.4-0.7
	- depth stratum	(1;6)-(4)	(1)-(6)	(6)-(5)	(2)-(1)
	- mean	5.0		1.1	0.5
April	1983	4 - 7	108-180	1.5-2.4	0.6-0.8
	- depth stratum	(5)-(1)	(5)-(3)	(5)-(1)	(4)-(1)
	- mean	5.4		1.6	0.7
March	1984	3 - 6	22-142	1.2-2.0	0.5-0.8
	- depth stratum	(2)-(3 to 6)	(2)-(3)	(2)-(5)	(3)-(2;5)
	- mean	5.4		1.6	0.7
November	1984	6 - 8	30-142	1.5-2.5	0.6-0.9
	- depth stratum	(1;2;4)-(3)	(1)-(5)	(2)-(5)	(2)-(5)
	- mean	6.6		2.0	0.7

Table V b. Range of community parameters per suvey.
Zone B: Bio Bio. Key: S = species number; C =
mean capture/trawl (kg); H' = diversity; J =
evenness (depth strata as shown in Table II).

Survey		S	C	H'	J
April	1982	2 - 3	26-70	0.4-1.0	0.2-1.0
	- depth stratum	(1;3)-(2)	(3)-(2)	(2)-(1)	(2)-(1)
	- mean	2.3		0.7	0.7
April	1983	2 - 6	72-152	0.3-1.6	0.2-0.6
	- depth stratum	(3)-(1)	(2)-(1)	(3)-(1)	(2)-(1)
	- mean	4.0		0.9	0.4
March	1984	1 - 2	7 - 34	0.0-0.6	0.0-0.6
	- depth stratum	(3)-(1;2)	(1)-(3)	(3)-(1)	(3)-(1)
	- mean	1.7		0.3	0.3
November	1984	5 - 6	39-209	1.2-2.1	0.5-0.8
	- depth stratum	(2)-(1;3)	(1)-(3)	(2)-(3)	(2)-(3)
	- mean	5.7		1.7	0.7

Table V c. Range of community parameter, per survey.
Zone E: Exterior. Key: S = species number; C =
mean capture/rawl (kg); H' = diversity; J =
evenness (depth strata as shown in Table II).

Survey	S	C	H'	J
April 1982	4 - 5	29-374	1.2-1.7	0.6-0.7
- depth stratum	(4)-(2;3;5)	(2)-(5)	(4)-(3;5)	(4)-(5)
- mean	4.8		1.6	0.7
April 1983	5	55-68	1.7-1.8	0.7-0.8
- depth stratum	(3;4)	(4)-(3)	(4)-(3)	(4)-(3)
- mean	5.0		1.8	0.8
March 1984	3 - 6	89-776	0.5-1.9	0.3-0.9
- depth stratum	(2)-(5)	(2)-(4)	(2)-(5)	(2)-(3)
- mean	4.5		1.3	0.6
November 1984	6 - 7	115-422	1.5-2.3	0.6-0.8
- depth stratum	(2;4)-(3)	(4)-(2)	(2)-(3)	(2)-(3)
- mean	6.3		1.8	0.7

Table VI. Similarity of biomass of demersal fish within and between depth strata and zones. The significance of difference of within vs. between CZ's was estimated using the Mann-Whitney U-test. The large sample approximation was used (ts; CONOVER, 1971). The statistical significance is shown by "*"; $\alpha = 0.025$.

Period		Mean CZ	s.d.	n	t_s	w(.975)	
a) April '82	within	.657	.148	73			
	between	.512	.207	66	3,468	2,646	*
b) April '83	within	.615	.171	68			
	between	.550	.191	45	1,881	591	*
c) March '84	within	.695	.175	64			
	between	.495	.238	66	3,220	2,234	*
d) Nov. '84	within	.581	.127	66			
	between	.480	.216	55	2,230	1,924	*

Table VII. Zones and depth strata with the most important species of fish (the sequence shows the order of importance). A = Achira; B = Bio Bio; E = Exterior. The numbers are depth strata, as ranged in Table II; Gr.= group created by the cluster analysis.

Survey	Gr.	Zone depth	Species
a) April '82	1	A1-B1	: <i>M. gayi</i> , <i>T. murphyi</i>
	2	A2-B2-A3-A4:	<i>M. gayi</i>
		B3	<i>M. gayi</i> , <i>G. maculatus</i> , <i>T. murphyi</i>
	3	A5-E3	: <i>M. gayi</i> , <i>C. aconcagua</i>
	4	E4	: <i>C. aconcagua</i> , <i>M. gayi</i>
	5	E5	: <i>C. aconcagua</i> , <i>M. gayi</i> , <i>E. crassicauda</i>
	6	E2	: <i>T. murphyi</i> , <i>H. macrops</i> , <i>M. gayi</i>

b) April '83	1	B2-B3	: <i>M. gayi</i>
		A2	<i>M. gayi</i> , <i>H. macrops</i> , <i>T. murphyi</i>
		A3	<i>M. gayi</i> , <i>H. macrops</i>
		A4	<i>M. gayi</i> , <i>E. crassicauda</i>
		A5	<i>M. gayi</i> , <i>C. aconcagua</i>
	2	A1	: <i>M. gayi</i> , others
		B1	<i>M. gayi</i> , others
	3	E3	: <i>C. aconcagua</i> , <i>M. gayi</i>
		E4	<i>M. gayi</i> , <i>C. aconcagua</i> , skates

(Table VII, cont.)

Survey	Gr.	Zone depth	Species
c) March '84	1	B1 B2-B3-E2	: <i>M. gayi</i> , <i>G. maculatus</i> <i>M. gayi</i>
	2	A3-A4-A5 E3	: <i>M. gayi</i> , <i>H. macrops</i> <i>M. gayi</i> , <i>H. macrops</i> , <i>T. murphyi</i>
	3	A2	: <i>T. murphyi</i> , <i>M. gayi</i>
	4	A6	: <i>C. aconcagua</i> , sharks, <i>H. macrops</i>
	5	E5	: <i>C. aconcagua</i> , <i>H. macrops</i>
	6	E4	: <i>H. macrops</i> , <i>C. aconcagua</i>

d) Nov. '84	1	A2-B2 A3 E2	: <i>M. gayi</i> , <i>H. macrops</i> <i>M. gayi</i> , <i>H. macrops</i> , <i>C. aconcagua</i> <i>M. gayi</i> , <i>C. aconcagua</i>
	2	A1 B1	: Others, <i>M. gayi</i> , <i>H. macrops</i> <i>M. gayi</i> , others
	3	A4 A5	: <i>M. gayi</i> , <i>C. aconcagua</i> <i>C. aconcagua</i> , <i>M. gayi</i> , <i>G. maculatus</i> , skates.
	4	B3 E3 E4	: <i>C. aconcagua</i> , skates, <i>M. gayi</i> <i>C. aconcagua</i> , skates, sharks <i>C. aconcagua</i> , sharks

Table VIII a. Prey taxa by weight (in percentage) in horse mackerel, *Trachurus murphyi*.

- Length range (cm): 23-44

- Nomenclature: TRA 1

Zone key : A=Achira; B=Bio Bio; E=Exterior

Cruise key: M=March; N=November

Prey key : j=juvenil

Prey taxa	A		B		E	
	M	N	M	N	M	N
Crustacea						
Megalopa		2				
Larvae indet.		2				
Decapoda						
<i>Pleuroncodes monodon</i> (j)		1				
Stomatopoda						
<i>Pterygosquilla armata</i>	4					
<i>P. armata</i> (j)		1				
Euphausiacea						
<i>Euphausia mucronata</i>	94	87	98		100	
Teleostei						
<i>Merluccius gayi</i> (j)	1					
Indeterminatae (j)		3				
No. prey taxa (> 1%)	3	6	1		1	
No. prey taxa (> 10%)	1	1	1		1	
Diversity (H')	.34	.7	0		0	
Sample size	14	111	25		15	

Table VIII b. Prey taxa by weight (in percentage) in cardinalfish, *Epigonus crassicauda*.

- Length range (cm): 22-37.

- Nomenclature : EPI 1

(see Table VIIIa for keys).

Prey taxa	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Heterocarpus reedi</i>	47					
Euphausiacea						
<i>Euphausia mucronata</i>	5	100				100
Teleostei						
<i>Merluccius gayi</i> (j)	41					
Indeterminatae	8					
No. prey taxa (> 1%)	4	1				1
No. prey taxa (> 10%)	2	1				1
Diversity (H')	1.6	0				0
Sample size	26	14				26

Table VIII c. Prey taxa by weight (in percentage) in Chilean hake, *Merluccius gayi*.
 - Length range (cm) : 13-66
 - Nomenclature : MER 1-4
 (see Table VIIIa for keys).

Prey taxa	MER 1 (17-25 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>		17		75		
<i>P. monodon</i> (j)	5	2	5	7		
<i>Austropandalus grayi</i>				1		
Stomatopoda						
<i>Pterygosquilla armata</i>				8		
<i>P. armata</i> (j)		2		1		
Euphausiacea						
<i>Euphausia mucronata</i>	29	14				
Polychaeta						
<i>Paraprionospio pinnata</i>		1				
Indeterminatae				1		
Teleostei						
<i>Merluccius gayi</i> (j)	66	2	84			
<i>Engraulis ringens</i>		45				
Indeterminatae		14				
Indeterminatae (j)				1 15		
No. prey taxa (> 1%)	3	8	5	5		
No. prey taxa (> 10%)	2	4	1	2		
Diversity (H')	1.1	2.2	0.8	1.1		
Sample size	24	24	17	21		

(Table VIII c, cont.)

Prey taxa	MER 2 (26-35 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	2	9	8	71		
<i>P. monodon</i> (j)			38		39	
<i>Cervimunida johni</i>		1	5			
<i>Austropandalus grayi</i>	3					
<i>Cancer coronatus</i>		2				
<i>C. porteri</i>		2				
Stomatopoda						
<i>Pterygosquilla armata</i>	1		3			
<i>P. armata</i> (j)	1		5			
Euphausiacea						
<i>Euphausia mucronata</i>	72	70	3	3	60	
Mollusca						
Gastropoda						
<i>Nassarius gayi</i>				2		
Teleostei						
<i>M. gayi</i> (j)	4		35			
<i>Coelorinchus aconcagua</i>		2				
<i>Engraulis ringens</i>	13	12		21		
Indeterminatae	5		1	2		
Indeterminatae (j)			1			
No. prey taxa (> 1%)	8	7	9	5	2	
No. prey taxa (> 10%)	2	2	2	2	2	
Diversity (H')	1.7	1.4	2.2	1.2	1.0	
Sample size	93	71	73	79	7	

(Table VIII c, cont.)

Prey taxa	MER 3 (36-50 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	15	34	21	59	61	6
<i>P. monodon</i> (j)	22	8	19		2	
<i>Heterocarpus reedi</i>		2				4
<i>Austropandalus grayi</i>	1					
<i>Cancer coronatus</i>			2			
<i>C. porteri</i>		4		1		
Indeterminatae					10	
Stomatopoda						
<i>Pterygosquilla armata</i>	7		6			
<i>P. armata</i> (j)	6		7			
Euphausiacea						
<i>Euphausia mucronata</i>	4	18	1	1	7	27
Mollusca						
Gastropoda						
<i>Nassarius gayi</i>				1		
Cephalopoda						
<i>Loligo gahi</i>			1			

(Table VIII c, cont.)

Prey taxa	MER 3 (36-50 cm)					
	A		B		E	
	M	N	M	N	M	N
Teleostei						
<i>Merluccius gayi</i>				1		
<i>M. gayi</i> (j)	11	14	29	7		
<i>Coelorinchus aconcagua</i>					50	
<i>Epigonus crassicauda</i>	10					
<i>Myctophidae</i>					1	
<i>Hippoglossina macrops</i>	4			1		
<i>Engraulis ringens</i>	17	13	7	22	11	
<i>Scomberesox saurus</i>				1		
<i>Bingamycthyx macrophos</i>			1			
Indeterminatae	2	6	7	2	20	
Indeterminatae (j)	1					
No. prey taxa (> 1%)	12	8	11	10	5	6
No. prey taxa (> 10%)	5	4	3	2	3	3
Diversity (H')	3.1	2.6	2.8	1.7	1.6	1.9
Sample size	108	211	78	401	17	20

(Table VIII c, cont.)

Prey taxa	MER 4 (51-66 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	61	54	9	68		
<i>P. monodon</i> (j)	4		2			
<i>Heterocarpus reedi</i>		5				
<i>Mursia gaudichaudii</i>			1			
<i>C. porteri</i>		1		1		
Stomatopoda						
<i>Pterygosquilla armata</i>	20		15	1		
<i>P. armata</i> (j)	4					
Euphausiacea						
<i>Euphausia mucronata</i>	4					
Teleostei						
<i>Merluccius gayi</i>				11		
<i>M. gayi</i> (j)	6		5	7		
<i>Epigonus crassicauda</i>		12				
<i>Hippoglossina macrops</i>		5				
<i>Engraulis ringens</i>		13		8		
<i>Scomberesox saurus</i>			66			
Indeterminatae		9	1	2		
No. prey taxa (> 1%)	6	7	7	7		
No. prey taxa (> 10%)	2	3	2	2		
Diversity (H')	1.7	2.0	1.6	1.7		
Sample size	9	40	32	41		

Table VIII d. Prey taxa by weight (in percentage) in black ling, *Genypterus maculatus*.

- Length range (cm): 32-80

- Nomenclature : GEN 1-2

(see Table VIIIa for keys).

Prey taxa	GEN 1 (32-50 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	51	29	87	47		22
<i>P. monodon</i> (j)		8				
<i>Cervimunida johni</i>				2		
<i>Heterocarpus reedi</i>	5					11
<i>Cancer coronatus</i>		2				
<i>C. porteri</i>		31		39		65
Indeterminatae		1				2
Stomatopoda						
<i>Pterygosquilla armata</i>	12	2	4			
Polychaeta						
<i>Spionidae</i>				2		
Teleostei						
<i>Merluccius gayi</i>				9		
<i>M. gayi</i> (j)			9			
<i>Scomberesox saurus</i>		23				
Indeterminatae	33	3				
No. prey taxa (> 1%)	4	8	3	5		4
No. prey taxa (> 10%)	3	3	1	2		3
Diversity (H')	1.6	2.3	0.7	1.6		1.4
Sample size	20	56	7	12		35

(Table VIII d, cont.)

Prey taxa	GEN 2 (51-80 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	8		47			
<i>Heterocarpus reedi</i>	1					
<i>Mursia gaudichaudii</i>	3		4			
<i>Cancer coronatus</i>			18			
<i>C. porteri</i>	56					
Stomatopoda						
<i>Pterygosquilla armata</i>	13		15			
<i>P. armata</i> (j)	1					
Teleostei						
<i>M. gayi</i> (j)			16			
Indeterminatae	18					
No. prey taxa (>, 1%)	7		5			
No. prey taxa (>, 10%)	3		4			
Diversity (H')	1.9		2.0			
Sample size	13		12			

Table VIII e. Prey taxa by weight (in percentage) in bigeye flounder, *Hipposglossina macrops*.
 - Length range (cm): 10-40
 - Nomenclature : HIP 1-3
 (see Table VIIIa for keys).

Prey taxa	HIP 1 (10-25 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	60	60		63	28	
<i>P. monodon</i> (j)	3	3		3	54	
<i>Austropandalus grayi</i>		2				
<i>Cancer coronatus</i>					5	
<i>C. porteri</i>		23		25		
Indeterminatae	1					
Stomatopoda						
<i>Pterygosquilla armata</i>	10	7		8		
Euphausiacea						
<i>Euphausia mucronata</i>	1					
Polychaeta						
<i>Paraprionospio pinnata</i>		1				
<i>Nephtys ferruginea</i>	2	2			3	
<i>Spionidae</i>	1					
Indeterminatae	8			1	1	
Teleostei						
<i>Merluccius gayi</i> (j)	1				3	
<i>Mictophidae</i>	2					
Indeterminatae	6				6	
Indeterminatae (j)	3					
No. prey taxa (> 1%)	12	7		5	7	
No. prey taxa (> 10%)	2	2		2	2	
Diversity (H')	2.1	1.6		1.4	1.8	
Sample size	51	43		19	17	

(Table VIII e, cont.)

Prey taxa	HIP 2 (26-30 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	34	62	89		80	8
<i>P. monodon</i> (j)		2	9		1	
<i>Cervimunida johni</i>					10	
<i>Heterocarpus reedi</i>	18					
<i>Mursia gaudichaudii</i>		1				
<i>C. porteri</i>		23	1			8
Stomatopoda						
<i>Pterygosquilla armata</i>	28	11			7	
Teleostei						
<i>Merluccius gayi</i> (j)					2	
<i>Coelorinchus aconcagua</i>						28
Indeterminatae	19					57
No. prey taxa (> 1%)	4	5	3		5	4
No. prey taxa (> 10%)	4	3	1		2	2
Diversity (H')	1.9	1.3	0.5		1.0	1.6
Sample size	20	50	45		15	7

(Table VIII e, cont.)

Prey taxa	HIP 3 (31-40 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	66	77		97	96	43
<i>P. monodon</i> (j)				1		
<i>Cervimunida johni</i>	25					
<i>Cancer coronatus</i>					2	
<i>C. porteri</i>		15		2		57
Stomatopoda						
<i>Pterygosquilla armata</i>	3	3			2	
Teleostei						
<i>Merluccius gayi</i> (j)	1					
<i>Hygophum bruumi</i>	3					
<i>Hippoglossina macrops</i>	2					
Indeterminatae (j)		4				
No. prey taxa (> 1%)	6	4		3	3	2
No. prey taxa (> 10%)	2	2		1	1	2
Diversity (H')	1.4	1.0		0.2	0.3	1.0
Sample size	30	48		47	27	8

Table VIII f. Prey taxa by weight (in percentage) in rattail, *Coelorinchus aconcagua*.

- Length range (cm): 20-38

- Nomenclature : COE 1

(see Table VIIIa for keys).

Prey taxa	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>		18		58		22
<i>P. monodon</i> (j)	5	14		7		43
<i>Austropandalus grayi</i>					4	
<i>Haliporoides diomedae</i>						2
<i>Cancer coronatus</i>		3				
<i>Libidoclaea granaria</i> (j)				4		
<i>Paguridae</i>					2	
Larvas indeterminatae	1				1	
Indeterminatae		3		4		2
Stomatopoda						
<i>Pterygosquilla armata</i>		4		1		
<i>P. armata</i> (j)	12	5		2	4	
Amphipoda						
<i>Monoculodes</i> sp.		8				
<i>Lilgeborgia</i> sp.					4	
Indeterminatae	11				11	
Euphausiacea						
<i>Euphausia mucronata</i>	14	16		2		20
Mysidacea	4				1	
Cumacea					6	
Ostracoda	7					
Polychaeta						
<i>Paraprionospio pinnata</i>		13		5		
<i>Nephtys ferruginea</i>	5	9		3	4	
<i>Diopatra</i> sp.					4	
<i>Onuphidae</i>		3			6	
Indeterminatae	32	13		13	26	8

(Table VIII f, cont.)

Prey taxa	A		B		E	
	M	N	M	N	M	N
Sipunculida					21	
Bivalvia					2	
Teleostei indet. (j)					1	
No. prey taxa ($\geq 1\%$)	10	11	10		15	6
No. prey taxa ($\geq 10\%$)	4	5	2		3	3
Diversity (H')	2.8	3.3	2.1		3.2	2.0
Sample size	44	65	28		27	37

Table VIII g. Prey taxa by weight (in percentage) in Chilean skate, *Raja chilensis*.
 - Length range (cm): 37-111
 - Nomenclature : RAJ 1-2
 (see Table VIIIA for keys).

Prey taxa	RAJ 1 (37-80 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	11	24	82		100	29
<i>Cervimunida johni</i>		11				7
<i>Heterocarpus reedi</i>	6	18				4
<i>Mursia gaudichaudii</i>			4			6
<i>Cancer coronatus</i>		4	2			13
<i>C. porteri</i>		26	10			39
<i>Libinia clava</i>	14					
Indeterminatae		10				
Stomatopoda						
<i>Pterygosquilla armata</i>	65	7				
Teleostei						
<i>Hippoglossina macrops</i>	5					
Indeterminatae			2			2
No. prey taxa (> 1%)	5	7	5		1	7
No. prey taxa (> 10%)	3	5	2		1	3
Diversity (H')	1.6	2.6	1.0		0	2.2
Sample size	14	12	57		9	20

(Table VIII g, cont.)

Prey taxa	RAJ 2 (81-111 cm)					
	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>		33			45	
<i>Cervimunida johni</i>					6	
<i>Heterocarpus reedi</i>	26	24				
<i>C. porteri</i>		26			2	
<i>Libidoclaea granaria</i>	71					
Indeterminatae		16				
Stomatopoda						
<i>Pterygosquilla armata</i>	3	2				
Teleostei						
Indeterminatae					47	
No. prey taxa (> 1%)	3	5			4	
No. prey taxa (> 10%)	2	4			2	
Diversity (H')	1.0	2.1			1.4	
Sample size	6	5			4	

Table VIII h. Prey taxa by weight (in percentage) in little skate, *Bathyraja* sp.
 - Length range (cm): 22-56
 - Nomenclature : BAT 1
 (see Table VIIIa for keys).

Prey taxa	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	13	35			68	
<i>P. monodon</i> (j)					2	
<i>Cervimunida johni</i>					1	
<i>Mursia gaudichaudii</i>	8	54			3	
<i>Cancer coronatus</i>					1	
<i>C. porteri</i>					12	
<i>Libidoclaea granaria</i>	20					
Indeterminatae					6	
Stomatopoda						
<i>Pterygosquilla armata</i>	59					
Euphausiacea						
<i>Euphausia mucronata</i>		2			7	
Polychaeta indeterminatae		7				
No. prey taxa (> 1%)	4	4			8	
No. prey taxa (> 10%)	3	2			2	
Diversity (H')	1.6	1.4			1.7	
Sample size	17	11			26	

Table VIII i. Prey taxa by weight (in percentage) in hooktooth dogfish, *Aculeola nigra*.

- Length range (cm): 23-66

- Nomenclature : ACU 1

(see Table VIIIa for keys).

Prey taxa	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	21				16	
<i>Heterocarpus reedi</i>	11				76	
<i>Mursia gaudichaudii</i>	5					
<i>Libidoclaea granaria</i>	2					
Stomatopoda						
<i>Pterygosquilla armata</i>	1				4	
Mollusca						
Cephalopoda						
<i>Loligo gahi</i>	1				5	
Teleostei						
<i>Hippoglossina macrops</i>	39					
Indeterminatae	20					
No. prey taxa (> 1%)	8				4	
No. prey taxa (> 10%)	4				2	
Diversity (H')	2.3				1.1	
Sample size	15				9	

Table VIII j. Prey taxa by weight (in percentage) in
combtooth dogfish, *Centroscyllium nigrum*.
- Length range (cm): 38-69
- Nomenclature : CEN 1
(see Table VIIIa for keys)

Prey taxa	A		B		E	
	M	N	M	N	M	N
Crustacea						
Decapoda						
<i>Pleuroncodes monodon</i>	15					
<i>Heterocarpus reedi</i>	27					
<i>Libidoclaea granaria</i>	8					
Stomatopoda						
<i>Pterygosquilla armata</i>	4					
Teleostei						
<i>Lampanyctus iselinoides</i>	41					
Indeterminatae	3					
No. prey taxa (> 1%)	6					
No. prey taxa (> 10%)	3					
Diversity (H')	2.0					
Sample size	37					

Table IX. Predator fish species, nomenclature, length range and total sample size used in this study.

Predator species	Nomenclature	length range (cm)	sample size
<i>Trachurus murphyi</i>	TRA 1	23 - 44	165
<i>Epigonus crassicauda</i>	EPI 1	22 - 37	66
<i>Merluccius gayi</i>	MER 1	17 - 25	86
	MER 2	26 - 35	323
	MER 3	36 - 50	835
	MER 4	51 - 66	122
<i>Genypterus maculatus</i>	GEN 1	32 - 50	130
	GEN 2	51 - 80	25
<i>Hippoglossina macrops</i>	HIP 1	10 - 25	130
	HIP 2	26 - 30	137
	HIP 3	31 - 40	160
<i>Coelorinchus aconcagua</i>	COE 1	20 - 38	201
<i>Raja chilensis</i>	RAJ 1	37 - 80	112
	RAJ 2	81 - 111	15
<i>Bathyraja</i>	BAT 1	22 - 56	54
<i>Aculeola nigra</i>	ACU 1	23 - 66	26
<i>Centroscyllium nigrum</i>	CEN 1	38 - 69	37

Table X. Mean values of feeding heterogeneity, revealed by average of H' , taking into account three zones and two surveys.

Predator species	length range (cm)	H'
<i>Trachurus murphyi</i>	23 - 44	0.3
<i>Epigonus crassicauda</i>	22 - 37	0.5
<i>Merluccius gayi</i>	17 - 25	1.3
	26 - 35	1.5
	36 - 50	2.3
	51 - 66	1.8
<i>Genypterus maculatus</i>	32 - 50	1.5
	51 - 80	2.0
<i>Hippoglossina macrops</i>	10 - 25	1.7
	26 - 30	1.3
	31 - 40	0.8
<i>Coelorinchus aconcagua</i>	20 - 38	2.7
<i>Raja chilensis</i>	37 - 80	1.5
	81 - 111	1.5
<i>Bathyraja</i>	22 - 56	1.6
<i>Aculeola nigra</i>	23 - 66	1.7

Table XI a. Similarity of diets of demersal fish within and between groups per zone, for samples collected during March 1984. The significance of difference of within vs. between size groups was estimated using the Mann-Whitney U-test. The large sample approximation was used (t_s ; CONOVER, 1971). The statistical significance is shown by "*"; $\alpha = 0.025$.

Zone		Mean CZ	s.d.	n	t_s	w(.975)	
Achira	within	.325	.392	256	19,974	18,012	*
	between	.195	.188	136			
Bio Bio	within	.304	.436	107	1,431	1,211	*
	between	.259	.184	21			
Exterior	within	.460	.468	60	1,363	1,155	*
	between	.215	.281	36			

Table XI b. Similarity of diets of demersal fish within and between groups per zone, for samples collected during November 1984. The significance of difference of within vs. between size groups was estimated with the Mann-Whitney U-test. The large sample approximation was used (t_s ; CONOVER, 1971). The statistical significance is shown by "*"; $\alpha = 0.025$.

Zone		Mean CZ	s.d.	n	t_s	w(.975)	
Achira	within	.431	.404	376	20,833	17,762	*
	between	.313	.233	91			
Bio Bio	within	.553	.422	394	10,714	11,345	NO
	between	.544	.274	55			
Exterior	within	.465	.339	72	1,538	1,383	*
	between	.256	.211	36			

Table XII a. Species composition of the trophic associations (TA), Achira zone (March 1984)

TA	Main prey taxa	Predator	Predator category
1	Crustaceans (<i>P. armata</i> <i>P. monodon</i> , <i>L. granaria</i>)	<i>Bathyraja</i> sp. (22-53 cm) <i>R. chilensis</i> (37-80 cm)	Benthic feeder
2	Crustaceans (<i>P. monodon</i> , <i>P. armata</i> , <i>C. johnei</i>) Fish (<i>H. macrops</i> , Teleostei)	<i>M. gayi</i> (51-66 cm) <i>H. macrops</i> (10-38 cm) <i>G. maculatus</i> (32-50 cm) <i>A. nigra</i> (23-50 cm)	Benthic feeder
3	Crustaceans (<i>H. reedi</i> , <i>L. granaria</i>) Lanternfish	<i>C. granulorum</i> (38-69 cm) <i>R. chilensis</i> (81-102 cm)	Benthic or bathypelagic feeder
4	Euphausiacea <i>E. ringens</i>	<i>M. gayi</i> (26-35 cm) <i>T. murphyi</i> (29-43 cm)	Pelagic feeder
5	<i>M. gayi</i> (postlarvae, juveniles) Euphausiacea	<i>E. crassicauda</i> (22-37 cm) <i>M. gayi</i> (13-25 cm)	Pelagic feeder

(Table XII a, cont.)

TA	Main prey taxa	Predator	Predator category
	Crustaceans (<i>C. porteri</i> , <i>P. armata</i>) Teleostei	<i>G. maculatus</i> (51-80 cm)	Benthic feeder
	<i>P. monodon</i> , <i>E. ringens</i>	<i>M. gayi</i> (36-50 cm)	Benthic- pelagic feeder
	Polychaeta, Euphausiacea, <i>P. armata</i> , Amphipoda	<i>C. aconcagua</i> (23-35 cm)	Benthic feeder

Table XII b. Species composition of the trophic associations (TA), Achira zone (November 1984)

TA	Mean prey taxa	Predator	Predator category
1	Crustaceans (<i>P. monodon</i> , <i>C. porteri</i> , <i>H. reedi</i>)	<i>H. macrops</i> (18-37 cm) <i>G. maculatus</i> (32-50 cm) <i>R. chilensis</i> (37-102 cm)	Benthic feeder
2	Crustaceans (<i>P. monodon</i>) Fish (<i>M. gayi</i> , <i>E. ringens</i> , <i>C. aconcagua</i>)	<i>M. gayi</i> (17-25 cm) <i>M. gayi</i> (36-66 cm)	Benthic- pelagic feeder
3	Euphausiacea	<i>E. crassicauda</i> (29-35 cm) <i>T. murphyi</i> (23-40 cm) <i>M. gayi</i> (26-35 cm)	Pelagic feeder
	Crustaceans (<i>M. gaudichaudii</i> , <i>P. monodon</i>)	<i>Bathyraja</i> sp. (28-50 cm)	Benthic feeder
	Crustaceans (<i>P. monodon</i> , Euphuasiacea) Polychaets	<i>C. aconcagua</i> (20-35 cm)	Benthic (-pelagic ?) feeder

Table XIII a. Species composition of the trophic associations (TA), Bio Bio zone (March 1984)

TA	Main prey taxa	Predator	Predator category
1	Fish (postlarvae, juveniles of <i>M. gayi</i>) Crustaceans (<i>P. monodon</i>)	<i>M. gayi</i> (16-50 cm)	Pelagic- benthic feeder
2	Crustaceans (<i>P. monodon</i> , <i>C. coronatus</i>)	<i>G. maculatus</i> (34-72 cm)	Benthic feeder
	Fish (<i>S. saurus</i>) Crustaceans (<i>P. armata</i> , <i>P. monodon</i>)	<i>M. gayi</i> (51-62 cm)	Pelagic- benthic feeder

Table XIII b. Species composition of the trophic associations (TA), Bio Bio zone (November 1984)

TA	Mean prey taxa	Predator	Predator catagory
1	Crustaceans (<i>P. monodon</i> , <i>C. porteri</i>)	<i>H. macrops</i> (22-40 cm) <i>M. gayi</i> (19-62 cm) <i>R. chilensis</i> (38-79 cm) <i>C. aconcagua</i> (21-38 cm) <i>G. maculatus</i> (40-90 cm)	Benthic feeder
	Euphausiacea	<i>T. murphyi</i> (27-35 cm)	Pelagic feeder

Table XIV a. Species composition of the trophic associations (TA), Exterior zone (March 1984)

TA	Main prey taxa	Predator	Predator category
1	Crustaceans (<i>P. monodon</i> , <i>C. porteri</i> , <i>C. johni</i>)	<i>H. macrops</i> (26-40 cm) <i>R. chilensis</i> (48-79 cm) <i>M. gayi</i> (36-49 cm)	Benthic feeder
2	Euphausiacea	<i>M. gayi</i> (26-35 cm) <i>T. murphyi</i> (32-43 cm)	Pelagic feeder
	Crustaceans (<i>P. monodon</i> , <i>C. porteri</i> , <i>P. armata</i>)	<i>H. macrops</i> (10-25 cm)	Benthic feeder
	Crustaceans (<i>P. monodon</i> , <i>H. reedi</i>)	<i>A. nigra</i> (38-50 cm)	Benthic feeder
	Polychaeta, Sipunculida, Amphipoda	<i>C. biconcavus</i> (23-35 cm)	Benthic feeder

Table XIV b. Species composition of the trophic associations (TA), Exterior zone (November 1984)

TA	Mean prey taxa	Predator	Predator category
1	Crustaceans (<i>C. porteri</i> , <i>P. monodon</i> , <i>H. reedi</i>)	<i>G. maculatus</i> (30-51 cm) <i>H. macrops</i> (31-41 cm) <i>R. chilensis</i> (48-79 cm)	Benthic feeder
2	Crustaceans (<i>P. monodon</i>)	<i>H. macrops</i> (26-30 cm) <i>R. chilensis</i> (92-111 cm)	Benthic feeder
	Crustaceans (<i>P. monodon</i> , <i>C. porteri</i>)	<i>Bathyraja</i> sp. (33-58 cm)	Benthic feeder
	Euphausiacea	<i>E. crassicauda</i> (21-36 cm)	Pelagic feeder
	Pisces (<i>C. bconcagua</i> , <i>E. ringens</i>) Euphausiacea	<i>M. gayi</i> (38-49 cm)	Pelagic- demersal feeder
	Crustaceans (<i>P. monodon</i> , Euphausiacea)	<i>C. bconcagua</i> (27-37 cm)	Benthic (-pelagic?) feeder

Table XV. Scores in fish species of the demersal assemblage off central Chile (SCORE = $\ln (w_i/w_j)$), where w_i = predator weight; w_j = weight of individual prey item; "%" is mean weight of prey item/predator mean weight, in percentage; n = sample size.

SPECIES		MARCH 1984	NOVEMBER 1984
<i>Merluccius gayi</i>			
mean score	:	6.3252	6.1140
s.d. of score	:	1.9488	2.1193
w_i/w_j	:	558	452
%	:	0.1792	0.2212
n	:	595	1,259
<i>Hippoglossina macrops</i>			
mean score	:	4.8978	5.7521
s.d. of score	:	1.7181	2.0757
w_i/w_j	:	134	315
%	:	0.7463	0.3175
n	:	181	353
<i>Genypterus maculatus</i>			
mean score	:	5.7407	5.4185
s.d. of score	:	1.1806	1.2220
w_i/w_j	:	311	226
%	:	0.3215	0.4425
n	:	54	135
<i>Coelorinchus aconcagua</i>			
mean score	:	9.0074	7.7424
s.d. of score	:	1.9026	2.2234
w_i/w_j	:	8,163	2,304
%	:	0.0123	0.0434
n	:	337	433

(Table XV, cont.)

SPECIES	MARCH 1984	NOVEMBER 1984
<i>Trachurus murphyi</i>		
mean score	:	9.6678
s.d. of score	:	2.4044
w_i/w_j	:	15,801
%	:	0.0063
n	:	447

Table XVI. Classification of *Merluccius gayi* by means of discriminant analysis.

a) March 1984

(percent of "grouped" cases correctly classified: 47%)

Actual range of length (cm)	No. of cases	Predicted group membership (cm)			
		(18-25)	(26-35)	(36-50)	(51-57)
(18 - 25)	24	75	25	0	0
(26 - 35)	93	42	48	8	2
(36 - 50)	108	24	26	39	11
(51 - 57)	9	0	11	33	56

b) November 1984

(percent of "grouped" cases correctly classified: 46%)

Actual range of length (cm)	No. of cases	Predicted group membership (cm)			
		(17-25)	(26-35)	(36-50)	(51-66)
(17 - 25)	24	29	54	17	0
(26 - 35)	71	6	76	15	3
(36 - 50)	222	2	46	36	16
(51 - 66)	40	0	10	45	45

Table XVII. Classification of *Hippoglossina macrops* by means of discriminant analysis.

a) March 1984

(percent of "grouped" cases correctly classified: 59%)

Actual range of length (cm)	No. of cases	Predicted group membership (cm)		
		(10-25)	(26-30)	(31-40)
(10 - 25)	51	66	20	14
(26 - 30)	20	35	55	10
(31 - 40)	30	7	30	63

b) November 1984

(percent of "grouped" cases correctly classified: 64%)

Actual range of length (cm)	No. of cases	Predicted group membership (cm)		
		(18-25)	(26-30)	(31-37)
(18 - 25)	43	42	35	23
(26 - 30)	50	6	76	18
(31 - 37)	47	0	30	70

Table XVIII. Shannon-Wiener Index (H'), as measure of feeding heterogeneity in fish species (*sensu* BERG, 1979).

(1): calculated from data of GALLARDO
et al. (1980).
(2): this work.

Fish species	(1)	(2)
<i>Coelorinchus aconcagua</i>	2.2	(2.0-3.3)
<i>Merluccius gayi</i>	2.1	(0.8-3.1)
<i>Genypterus maculatus</i>	1.6	(0.7-2.3)
<i>Hippoglossina macrops</i>	1.5	(0.2-2.1)
<i>Trachurus murphyi</i>	1.5	(0.0-0.7)
<i>Epigonus crassicauda</i>	0.9	(0.0-1.6)

Table XIX. *Merluccius gayi*. Mean weight of prey (*P. monodon*), $\bar{W}$, in percent of predator body weight (% BW); s.d.= standard deviation; n = number of samples (prey weights are the observed weights in the stomachs).

a) MARCH 1984

Time (hour)	$\bar{W}$	s.d.	n	Moving average
07	0.796	0.911	14	
				0.81
08	0.824	1.263	45	
				0.63
09	0.445	0.597	19	
				0.43
10	0.414	0.443	12	
				0.59
11	0.763	2.250	20	
				0.68
12				
13	0.593	0.802	7	
				0.92
14	1.256	1.757	9	
				1.10
15	0.949	1.170	16	
				1.06
16	1.181	1.288	33	
				1.42
17	1.656	1.431	9	
				0.85
18	0.051	0.032	6	
				0.46
19	0.873	1.185	18	

b) NOVEMBER 1984

Time (hour)	$\bar{W}$	s.d.	n	Moving average
07	1.898	1.381	14	
				1.19
08	0.491	0.492	6	
				0.69
09	0.895	1.049	51	
				0.69
10	0.484	0.504	74	
				0.73
11	0.969	1.025	52	
				0.70
12	0.428	0.400	15	
				0.83
13	1.223	0.893	42	
				1.20
14	1.173	1.118	41	
				1.29
15	1.414	1.532	57	
				1.12
16	0.826	1.084	56	
				0.67
17	0.506	0.409	78	
				0.59
18	0.683	0.503	35	
				0.81
19	0.946	0.981	37	

Table XX. *Merluccius gayi*. Daily ration (DR) and consumption of *P. monodon* (C), calculated from equations (2) and (6). $\bar{W}$ = initial mean weight of food ingested (% BW); N_f = number of stomachs containing *P. monodon*; N_t = number of stomachs sampled; B = biomass of predator. OTUs as defined in text.

a) MARCH 1984.

Instantaneous coefficient of gastric evacuation ($R = 0.1308$) was calculated from equation (3); water temperature = 10 °C; mean depth = 198 m. Digestion time (DT = 1.246 days) was calculated from equation (1).

OTU	$\bar{W}$	N_f	N_t	DR(%BW)	B(t)	C (t/month)
2	0.6944	55	299	0.1025	426.0	13.1
3	0.6540	103	596	0.0907	958.1	26.1
4	0.8469	19	195	0.0662	152.5	3.0
TOTAL		177	1,090		1,536.6	42.2

(Table XX, cont.)

b) NOVEMBER 1984.

R = 0.140; water temperature = 10.5 °C; mean depth = 133 m; DT = 1.160 days

OTU	$\bar{W}$	N_f	N_t	DR(%BW)	B(t)	C (t/month)
2	1.8458	61	283	0.3430	469.1	48.3
3	2.1261	299	1,192	0.4598	1,055.1	145.5
4	1.5504	45	154	0.3906	167.9	19.7
TOTAL		405	1,629		1,692.1	213.5

Table XXI. *Hippoglossina macrops*. Mean weight of prey (*P. monodon*), $\bar{W}$, in percent of predator body weight (%BW); s.d.= standard deviation; n = number of samples (prey weights are the observed weights in the stomachs).

a) MARCH 1984

Time (hour)	$\bar{W}$	s.d.	n	Moving average
06	4.313	4.814	8	
				3.13
07	1.950	0.798	5	
				1.40
08	0.828	0.825	3	
09				
				1.90
10				
11				
12	2.965	2.853	8	
13				2.24
14	1.513	0.959	10	
				2.11
15	2.710	2.259	12	
16				2.30
17	1.889	1.242	12	
				4.11
18	6.338	2.577	3	

b) NOVEMBER 1984

Time (hour)	$\bar{W}$	s.d.	n	Moving average
06	2.073	0.862	4	
				1.92
07	1.769	2.160	7	
				1.91
08	2.045	1.669	6	
				1.48
09	0.910	1.431	22	
				1.30
10	1.684	1.349	21	
11				
				1.54
12				
13	1.398	1.175	10	
				1.93
14	2.461	1.742	10	
				2.17
15	1.870	2.464	13	
				1.53
16	1.188	1.695	33	
				0.96
17	0.729	0.659	14	
				1.92
18	3.115	1.668	13	

Table XXII. *Hippoglossina macrops*. Daily ration (DR) and consumption of *P. monodon* (C), calculated from equations (2) and (6). $\bar{W}$ = initial mean weight of food ingested (%BW); N_f = number of stomachs containing *P. monodon*; N_t = number of stomach sampled; B = biomass of predator. OTUs as defined in text.

a) MARCH 1984.

R = 0.1308; water temperature = 10 °C; mean depth = 198 m; DT = 1.246 days.

OTU	$\bar{W}$	N_f	N_t	DR(%BW)	B(t)	C (t/month)
1	4.071	17	265	0.2096	761.4	47.9
2	4.071	18	100	0.5881	800.6	141.2
3	4.071	26	116	0.7323	1,966.0	438.5
TOTAL		61	481		3,558.0	627.6

b) NOVEMBER 1984.

R = 0.140; water temperature = 10.5 °C; mean depth = 133 m; DT = 1.16 days.

OTU	$\bar{W}$	N_f	N_t	DR(%BW)	B(t)	C (t/month)
1	3.43	27	277	0.2882	71.4	6.2
2	3.43	53	328	0.4778	187.5	26.5
3	3.43	63	317	0.5876	345.3	60.9
TOTAL			922		604.2	93.6

Appendix 1. List of the most important species of fish and crustaceans of Chile referenced in this work.

FISH SPECIES	COMMON NAME (English; Local)
<i>Aculeola nigra</i>	Hooktooth dogfish; tollo negro
<i>Bathyraja</i> sp.	Skate; raya
<i>Callorinchus callorinchus</i>	Elephantfish; peje gallo
<i>Centroscyllium nigrum</i>	Combtooth dogfish; tollo negro
<i>Coelorinchus aconcagua</i>	Rattail; peje rata
<i>Engraulis ringens</i>	Peruvian anchovy; anchoveta
<i>Epigonus crassicauda</i>	Cardinal fish; besugo
<i>Genypterus maculatus</i>	Black ling; congrio negro
<i>Hippoglossina macrops</i>	Bigeye flounder; lenguado ojos grandes
<i>Merluccius gayi</i>	Chilean hake; merluza común
<i>Prolatilus jugularis</i>	Pacific sandperch; blanquillo
<i>Raja chilensis</i>	Chilean skate; raya volantin
<i>Scomberesox saurus</i>	South Pacific saury; agujilla

(Appendix 1, cont.)

CRUSTACEANS	SPECIES	COMMON NAME (English; Local)
	<i>Cancer coronatus</i>	Crab; jaiba
	<i>Cancer porteri</i>	Crab; jaiba
	<i>Cervimunida johni</i>	Yellow shrimp; langostino amarillo
	<i>Heterocarpus reedi</i>	Pink shrimp; camarón nailon
	<i>Libinia clava</i>	Spider crab; jaiba araña
	<i>Mursia gaudichaudii</i>	Crab; jaiba
	<i>Pleuroncodes monodon</i>	Red shrimp; langostino colorado
	<i>Pterygosquilla armata</i>	Mantis shrimp; pateador

Appendix 2. Notes about the Discriminant Analysis and its use to classify predator fish.

Discriminant analysis (DA) is a statistical technique in which linear combinations of variables are used to distinguish between two or more categories of cases. The variables "discriminate" between groups of cases and predict into which category or group a case falls, based upon the values of these variables. The first task of DA is to find the linear combination of variables that best discriminates between, or separates, groups. After the discriminant functions have been computed, the coefficients can be used to classify all cases or only those cases for which group membership is unknown.

Although the variables are interrelated and we will to employ statistical techniques that incorporate these dependences, it is often helpful to begin analysing the differences between groups by examining univariate techniques. The equality of group means for each variable is tested with the F-test. If the observed significance level is small (less than 0.05), the hypothesis that all group means are equal is rejected.

Descriptive statistics and univariate tests of significance provide basic information about the distributions of the variables in the groups and help identify some differences among the groups. However, in DA and other multivariate statistical procedures, the emphasis is on analyzing the variables together, not one at a time.

It was said that in DA, a linear combination of the independent variables is formed and serves as the basis for assigning cases to groups. Thus, information contained in multiple independent variables is summarized in a single index. For example, by finding a weighted average of variables such as prey taxa, it can be obtained a score that distinguishes predator fish of several size classes (by length). In DA, the weights are estimated so that they result in the "best" separation between groups (= size classes of predator fish).

The linear discriminant equation for one group is

$$D_i = a_{i0} + a_{i1} X_1 + a_{i2} X_2 + \dots + a_{ip} X_p$$

where D_i is the classification score for group i , the a_{ij} 's are the classification coefficients estimated from the data, a_{i0} is the constant, and the X_j 's are the values of the independent (discriminating) variables.

A case is classified into the group that produces the highest classification score. For three groups, it must be computed three linear combinations for each case in the sample.

Therefore, the a 's are chosen so that the values of the discriminant function differ as much as possible between the groups, or that for the discriminant scores the ratio

between-groups sum of squares/within-groups sum of squares is a maximum. Any other linear combination of the variables will have a smaller ratio.

For cases included in the computation of the discriminant function, actual group membership is known and can be compared to that predicted using the discriminant function. For each group, the "Confusion Matrix" with classification results (Tables XVI and XVII) shows the numbers of corrected and incorreced classifications. Correctly classified cases appear on the diagonal of the table since the predicted and actual groups are the same.

Appendix 3. CURRICULUM VITAE

NAME : Hugo Gonzalo ARANCIBIA Farias
BIRTHDAY : October 4th, 1955
BIRTHPLACE : Santiago de Chile
NATIONALITY : Chilean

1961 - 1972 : Primary and secondary school, Santiago.
1973 - 1975 : Public officer at the Servicio de Equipos
Agrícolas Mecanizados.
1976 - 1982 : Undergraduate course in Marine Biology.
University of Concepcion, Chile.

TEACHING ACTIVITIES

1980 - 1982 : Student Assistant in Zoology of Invertebrates
I and III; Zoology of Vertebrates; Evolution;
Ichthyology; and Multivariate Analysis at the
University of Concepcion.
1984 : Teaching Assistant Course Biology of Verte-
brates. Department of Ecology, University of
Chile.
from 1985 : Assistant Professor at the Department of
Marine Sciences, University Arturo Prat,
Iquique (Chile).
1986 : Teaching Course of Ichthyology. National
Museum of Nature Sciences.

RESEARCH ACTIVITIES

1981 : Assistant of the Project "Growth and Age in
Red Shrimp *Pleuroncodes monodon*". Fisheries
Development Institute/University of Concep-
cion.
1983 : Adviser Fishery "Interpesca". Punta Arenas
(Chile).
1984 : Assistant in the "Red Shrimp Survey - 1984".
Undersecretariat of Fisheries / Fisheries
Development Institute.
: Adviser Undersecretariat of Fisheries Project
"First Spawning Size in *Octopus vulgaris*".

- 1985 : Head of Project "Trophic Ecology of *Sardinops sagax* in the Fishing Area of Iquique". University Arturo Prat / Fisheries Development Institute.
- : Head of Project "Fishery Biology of *Octopus vulgaris*". University Arturo Prat.

POST-GRADUATE STUDIES

- 1981 : Course in Population Ecology of Fish. University of Concepcion.
- 1982 : Course in Gonadic Histology of Fish. German-Peruvian Research Program/Peruvian Sea Institute.
- : Course in Coastal and Estuarine Process. University of Concepcion.
- : Course in Fishery Biology. Catholic University at Talcahuano.
- 1985 : Course in Pedagogy. University Arturo Prat.
- : Course in Remote-Sensing Applied to Oceanography. University Arturo Prat.
- : Coordinator Course in Egg Production Method for the Estimation of the Biomass of Peruvian Anchovy and Chilean Sardine. University Arturo Prat.
- 1987 : Course in Modelling and Management of Marine Systems. Royal School of Pharmacy, Copenhagen.
- : Course in Statistical Methods in Ecology. Biometry Society of the Federal Republic of Germany, Hamburg.
- 1988 : Course in Analysis of Fisheries Populations. University College of North Wales at Bangor.
- : Course in Population Dynamic of Fish - New Methods and Concepts. University of Kiel.
- : Course in New Methods for Spawning Biomass Estimates of Fish. AWI, Bremerhaven.

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- ARANCIBIA, H. & H. ROBOTHAM. 1984. Crecimiento y edad en el calamar patagónico (*Loligo gahi*). Inv. Pesq. (Chile) 31:71-79.
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- ARANCIBIA, H. 1988. Cluster analysis: the use of a simple statistical method in the identification of groups. ICES C.M./D:12. Statistics Cttee., Ref. Demersal Fish Cttee., 18 p.

OTHERS

- 1986 : Course in German Language at the Goethe Institute, Göttingen, FRG.

